POLLEN CHARACTERS IN RELATION TO THE DELIMITATION OF MYRTALES[1]

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ABSTRACT

Pollen grains representative of the Lythraceae (including subfamilies Punicoideae, Sonneratioideae, and Duabangoideae), Trapaceae, Oliniaceae, Combretaceae, Alzateaceae, Rhynchocalycaceae, Penaeaceae, Crypteroniaceae, Melastomataceae, Myrtaceae (including Psiloxylaceae and Heteropyxidaceae), and Onagraceae, the 11 families constituting the order Myrtales, were examined with scanning (SEM) and transmission (TEM) electron microscopy. With omission of the Trapaceae, Myrtaceae, and Onagraceae, the remaining families have enough similarities to be grouped together palynologically. Heterocolpate pollen characterizes the Lythraceae, Rhynchocalycaceae, Combretaceae, Oliniaceae, Penaeaceae, Crypteroniaceae, and Melastomataceae. In the latter five families, subsidiary colpi (pseudocolpi) were noted in all taxa examined except *Adelobotrys, Allomorphia, Astronia, Bredia, Oxyspora,* and *Tococa* of the Melastomataceae and *Buchenavia, Laguncularia,* and *Strephonema* of the Combretaceae. With the exceptions of the latter four genera these taxa possess intercolpar concavities. Subsidiary colpi and intercolpar concavities are considered to be functionally equivalent, their distinction being the larger size of the intercolpar concavities. Subsidiary colpi are equal to the number of apertures except in Lythraceae where *Ammannia, Nesaea,* and *Crenea* have twice the number; intercolpar concavities are also isomerous with apertures. In Oliniaceae, the subsidiary colpi are located on just one polar face and hence considered as half subsidiary colpi while Alzateaceae may have incipient subsidiary colpi. The pollen of Lythraceae subfamilies Sonneratioideae, Duabangoideae, and Punicoideae possess meridional ridges which alternate with the apertures; they are prominent in the former two subfamilies and weakly defined in the latter. Meridional ridges are also present in some Lythraceae lacking subsidiary colpi.

Exine sculpturing in the mesocolpia is variable throughout the order with Crypteroniaceae, Alzateaceae, Oliniaceae, and Penaeaceae basically psilate; Melastomataceae basically striate and rugulate; Combretaceae echinate, reticulate, rugulate, striate, and psilate; Lythraceae subfam. Lythroideae striate, psilate, verrucate, and granular; Lythraceae subfam. Punicoideae basically granular-microrugulate; and Lythraceae subfam. Sonneratioideae and Duabangoideae basically verrucate-rugulate. Commonly, the subsidiary colpi (and intercolpar concavities) and colpi have different sculpturing than the mesocolpial regions. Exine structure is essentially of the post and beam construction with the fundamental ektexine and endexine stratification layers. In all Combretaceae and some Melastomataceae the foot layer is strikingly delineated as domes, whereas in Alzateaceae the columellae layer follows a zig-zag course. The Oliniaceae and Penaeaceae are distinct throughout the order with remarkably thickened tectum and foot layer and negligible columellae; *Acanathella* of the Melastomataceae is somewhat similar, differing only in a better developed columellae layer.

In general, Lythraceae have the most diverse pollen at both sculptural and structural levels; Combretaceae also have considerable diversity, primarily exomorphically, and *Strephonema* is the only taxon noted in the order with a reticulate sculpture; Melastomataceae are diverse exomorphically, with the pollen of *Miconia melanotricha* shed as tetrads and that of *Tococa spadiciflora* as polyads, the only example of polyads in the order other than *Ludwigia* (Onagraceae); Oliniaceae, Penaeaceae, and Crypteroniaceae show rather uniform intrafamilial morphology. The monogeneric Trapaceae with protruding and domed apertures and meridional ridges resulting from exine folds is totally unique in Myrtales. One sample shows linked pollen grains suggestive of polyads while sections through the ridge area show an extremely thick endexine and loosely organized ektexine reminiscent of some Onagraceae. Myrtaceae, with pollen oblate-elliptic in lateral view and triangular in polar view, are also without a counterpart in Myrtales. Based on the nature of the colpi, three distinctive pollen groups are evident: (1) longicolpate, (2) syncolpate and parasyncolpate with and without intercolpar concavities, and (3) brevicolpate and brevissimicolpate. *Myrtus communis* and *Psidium littorale* shed pollen in tetrads as well as in monads and are the only tetrads recorded in Myrtales other than Onagraceae and *Miconia melanotricha* (Melastomataceae). The pollen morphology of *Psiloxylon* and *Heteropyxis,* genera of questionable taxonomic placement, suggests that they fit within the Myrtaceae. The final family, Onagraceae, is also very distinctive in Myrtales. The viscin threads, tetrads and polyads,

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exceptionally thick endexine, essentially spongy-paracrystalline ektexine with columellae absent or greatly reduced, absent foot layer, protruding apertures, and 2-aperturate grains (in *Fuchsia*) distinguish this family, which with a few superficial similarities to Trapaceae and Penaeaceae differs from all others in Myrtales.

Pollen morphology in the core families of the Myrtales as recognized by Dahlgren and Thorne (1984) has received surprisingly little study. The very extensive reference citations given in the four monumental pollen bibliographic indices of Thanikaimoni (1972, 1973, 1976, 1980) for these families include *all* studies in which pollen morphology is mentioned (e.g., atlases; regional and local floras; anatomical and embryological reports; horticultural, agricultural and geological records; chemical systematics, etc.), but relatively few of them are actually based on comprehensive pollen investigative research. Of those emphasizing pollen morphology, about 90% are confined to light microscopy (LM). Scanning electron microscopy (SEM) was utilized to a limited degree and, remarkably, structural data from transmission electron microscopy (TEM) (with the exception of Muller, 1973, 1975, 1978a, 1981; Lugardon & van Campo, 1978; Gadek & Martin, 1981, 1982; Skvarla et al., 1975, 1976; Skvarla et al., 1978) are virtually non-existent in the order. Furthermore, there are noticeably few modern studies in the three largest families, Melastomataceae, Combretaceae, and Myrtaceae, although the latter is currently under intensive examination by Gadek and Martin (1981, 1982, pers. comm.).

In this report we have attempted to provide a pollen morphologic overview of the major taxa in the core families (i.e., Lythraceae, including subfamilies Punicoideae, Sonneratioideae, and Duabangoideae; Trapaceae, Oliniaceae, Combretaceae, Alzateaceae, Rhynchocalycaceae, Penaeaceae, Crypteroniaceae, Melastomataceae, Myrtaceae including *Psiloxylon* and *Heteropyxis*, and Onagraceae). Our emphasis is on the exomorphic characters as revealed by SEM, however, this is supplemented in large part by structural information obtained by TEM.

MATERIALS AND METHODS

Most pollen was treated by the acetolysis method of Erdtman (1960). In some samples 5% KOH treatment followed acetolysis. For SEM, acetolyzed pollen was either critical point dried or air dried from 95% ethanol, sputter coated with gold, and examined with an ISI Super II SEM. For TEM, acetolyzed pollen was processed according to previously described methods (Skvarla, 1966) and examined with a Philips model 200 TEM. Some Onagraceae pollen was examined by TEM without acetolysis, that is, either freshly collected in 2.5% glutaraldehyde in 0.1 M cacodylate buffer at pH 7.2, or after rehydration from herbarium sheets. In both, subsequent processing basically followed earlier techniques (Skvarla, 1973). Pollen was examined with LM primarily to determine the nature of colpi and endoapertures.

Table 1 lists taxa examined, collecting information, ubiquity of subsidiary colpi, figure references, and select morphologic data.

The organization of this report is such that the core families are given individual discussion to include (1) general palynology, (2) specific morphology for taxa listed in Table 1, (3) a brief review of previous studies when relevant, and (4) significant morphological correlations with other core families. Following this treatment of the core families an attempt is made to summarize as well as synthesize the data for the entire order. Plate legends, in addition to being descriptive, frequently cite other reports in order to provide as complete a background as possible.

TERMINOLOGY

The terms used in this study to describe pollen grain morphology are essentially those of Erdtman (1971) for exomorphology and Faegri and Iversen (1975) for endomorphology. Although most are standard palynological jargon and therefore not in need of clarification, a few are particularly crucial to describing Myrtales pollen and are therefore discussed below.

1. *Subsidiary colpi* (*pseudocolpi*). According to Faegri and Iversen (1964: 225) a "Pseudocolpus (pseudopore): differs from a normal furrow (pore) in that it is not an exit for the pollen tube," while the definition of Erdtman (1971: 467) is "Colpoid streaks not functioning as apertures." Muller (1981) considers the term to be a misnomer because pseudocolpi function in volume changes of the pollen grain during expansion and contraction in response to moisture content (i.e., harmomegathy of Wodehouse, 1935),

TABLE 1. Pollen examined. (The parentheses ( ) in the column for subsidiary colpi mean that intercolpar concavities are recognized. Unless stated otherwise, all pollen grains are tricolporate.)

Taxon	Locality	Collector	Herbarium	Subsidiary Colpi	SEM-TEM	Figure No.	Remarks
LYTHRACEAE							
subfam. Lythroideae							
Ammannia coccinea Rottb.	California, USA	*Twisselman 7983*	KE	6	TEM	5B	
A. robusta Keer & Regel	Oklahoma, USA	*Waterfall 3027*	OKL	6	SEM, TEM	2A, B, 5A	
Crenea surinamensis L.	Guyana	*de la Cruz 3301*	MO	6	SEM	1F	Meridional ridge
Cuphea carthagenensis (Jacq.) MacBr.	Guatemala	*Aguilar 104*	OKL	0	SEM	2C	Tectal ridges
C. nitidula HBK.	Mexico	*Graham 614*	KE	0	TEM	5D	Tectal ridges
C. petiolata (L.) Koehne	Arkansas, USA	*Demaree 40737*	OKL	0	SEM	2D–F	Variable striate sculpture
C. racemosa (L.f.) Spreng.	Veracruz, Mexico	*Graham 689*	KE	0	TEM	5C	
Diplusodon villosus Pohl	Brazil	*Irwin et al. 26402*	MO	0	SEM, TEM	3A, B, 6E	Tricolpoidorate, colpus very short
Heimia salicifolia (HBK.) Link	Mexico	*Graham 141*	KE	0	TEM	5G	
H. salicifolia (HBK.) Link	Mexico	*Ventura 2430*	MO		SEM	1C–E	Rarely dicolporate and syncolpate
Lafoënsia punicifolia DC.	Chiapas, Mexico	*Breedlove 40657*	MO	0	SEM, TEM	3D–F, 5E, F, 6A	Meridional ridges, apertural fields and polar caps
Lagerstroemia speciosa (L.) Pers.	Honduras, cultivated	*Lent 4*	OKL	0	SEM	3C	Meridional ridges
Nesaea schinzii Koehne	Bulawayo Distr., Rhodesia	*Best 395*	MO	6	SEM	1A, B	
subfam. Punicoideae							
Punica granatum L.	Iran	*Antonio s.n.*	OKL	0	—	—	
P. granatum L.	Iran	*Grant 15704*	MO	0	SEM, TEM	7A, B, 8A	Weak meridional ridges
P. protopunica	Yemen, Socotra	*Smith & Lavranos 730*	K	0	SEM, TEM	7C–G, 8B, C	Meridional ridges

TABLE 1. Continued.

Taxon	Locality	Collector	Herbarium	Subsidiary Colpi	SEM-TEM	Figure No.	Remarks
subfam. Duabangoideae							
Duabanga moluccana Bl.	Los Banos, Philippines	*Elmer 18275*	MO	0	SEM	4F	Triporate, meridional ridges, apertural fields, polar caps
subfam. Sonneratioideae							
Sonneratia caseolaris Druce	Mahe Island, Seychelles	*Sauer 3808*	MO	0	SEM	4E	Triporate, meridional ridges, apertural fields, polar caps
TRAPACEAE							
Trapa japonica Flerov	Japan	*Boufford et al. 19962*	MO	0	SEM, TEM	10A–D, 11D	Meridional ridges over apertures
T. natans L.	unknown	Reverchon herbarium	MO 2532983	0	SEM	10E	Meridional ridges over apertures
T. natans L.	Germany	*Engelmann s.n.*	MO	0	SEM, TEM	9A, B, 10F, 11A	Meridional ridges over apertures
T. natans L.	New York, USA	*House 21708*	MO	0	SEM, TEM	9C–F, 11B, C	Meridional ridges over apertures; polyads
OLINIACEAE							
Olinia emarginata Burtt Davy	Natal, South Africa	*Hillard & Burtt 8691*	MO	3 (½)	SEM, TEM	13A–D, 14E	Asymmetric colpi, half subsidiary colpi
O. radiata Hofmeyr & Phill.	Zululand	*Wylie 8822*	K	3 (½)	SEM	12A–C	Asymmetric colpi, half subsidiary colpi
O. rochetiana A. Juss.	Malawi	*Chapman 996*	MO	3 (½)	SEM, TEM	12D–F, 14A	Asymmetric colpi, half subsidiary colpi
O. rochetiana A. Juss.	Mt. Meru, Tanzania	*Greenway & Fitzgerald 14970*	MO	3 (½)	TEM	14D	Asymmetric colpi, half subsidiary colpi
O. vanguerioides E. G. Baker	Rhodesia	*Chase 6774*	K	3 (½)	–		Asymmetric colpi, half subsidiary colpi
O. ventosa (L.) Cufod.	Cape Province, South Africa	*Fries et al. 660*	MO	3 (½)	SEM, TEM	13E, F, 14B, C	Asymmetric colpi, half subsidiary colpi

TABLE 1. Continued.

Taxon	Locality	Collector	Herbarium	Subsidiary Colpi	SEM-TEM	Figure No.	Remarks
COMBRETACEAE							
Anogeissus acuminata Wall.	Burma	*Po Chin 6100*	MO	3	SEM	18D, F	Echinate surface
Buchenavia suaveolens Eichler	Amazonas, Brazil	*Gentry & Ramos 12906*	MO	0	SEM	18A–C	Echinate surface
Bucida macrostachya Standl.	Chiapas, Mexico	*Breedlove 25160*	MO	3	SEM, TEM	17A, 21B	
Calycopteris floribunda (Roxb.) Poir.	Mysore, India	*Saldanha 16363*	MO	3	SEM	15G	
Combretum cacoucia Exell	Stann Creek Distr., Belize	*Dwyer et al. 552*	MO	3	SEM	15A–C	
C. farinosum HBK.	Sinaloa, Mexico	*Boke & Florantos 1*	OKL	3	SEM, TEM	16D, 20B, C	
C. laxum Jacq.	Loma Tequerre, Brazil	*Duke 10994* (3)	MO	3	SEM, TEM	16E, G, 20A	
C. trifolium Vent.	Vietnam	*Squires 792*	MO	3	SEM	16F	
Conocarpus erecta L.	Sinaloa, Mexico	*Waterfall 16249*	OKL	3	SEM, TEM	17B, 20E	
Guiera senegalensis Lam.	Cameroun	*Leeuwenberg 7485*	MO	3	SEM	18E	
Laguncularia racemosa (L.) Gaertn.	Costa Rica	*Croat 593 A*	MO	0	SEM	19E, F	
Lumnitzera racemosa Willd.	Eastern Province, Sri Lanka	*Davidse 7545*	MO	3	SEM, TEM	19D, 21C	
Poivrea coccinea DC.	Tulear Prov., Madagascar	*Croat 31768*	MO	3	SEM	19C	
Pteleopsis myrtifolia (Laws.) Engl. & Diels	Wankie Distr., Zimbabwe	*Raymond 130*	MO	3	SEM	17C	
Quisqualis indica L.	Laguna, Philippines	*Quisumbing Q-2160*	OKL	3	SEM	15F	
Q. parviflora (Ridl.) Exell.	Malaya	*Stone 9082*	MO	3	SEM	16H, I	
Q. pellegriniana (Exell.) Exell.	Zaire	*Grant 4048*	MO	3	TEM	21D	
Ramatuella argentea Kunth	Venezuela	*Maguire et al. 41879*	MO	3	SEM	17E, G	
Strephonema pseudocola A. Chev.	Tchien Distr., Liberia	*Baldwin 8007*	MO	0	SEM, TEM	19A, B, 21A	Reticulate surface
Terminalia catappa L.	Tulear Prov., Madagascar	*Croat 30941*	MO	3	SEM	17F	

TABLE 1. Continued.

Taxon	Locality	Collector	Herbarium	Subsidiary Colpi	SEM-TEM	Figure No.	Remarks
T. edulis Blanco	Luzon, Philippines	*Bernardo 23688*	MO	3	TEM	20D	
T. edulis Blanco	Laguna, Philippines	*Quisumbing 2156*	OKL	3	SEM	17D	
T. oblonga (R. & P.) Pois.	Colombia	*Renteria-Arriaga et al. 1889*	MO	3	SEM	16A–C	
Thiola inundata Ducke	Amazonas, Brazil	*Ducke 644*	MO	3	SEM	15D, E	Echinate surface
RHYNCHOCALYCACEAE							
Rhynchocalyx lawsonioides Oliv.	Natal, South Africa	*Nicholson s.n.*	MO	3	SEM, TEM	4A, C, 6D	
ALZATEACEAE							
Alzatea verticillata Ruiz & Pav.	Mendoza, Peru	*Woytkowski 8331*	MO	0	SEM, TEM	4B, D, 6B, C	
PENAEACEAE							
Brachysiphon acutus (Thunb.) A. Juss.	South Africa	*Dahlgren & Strid 3387*	LD	–	TEM	27B	
B. fucatus (L.) Gilg.	South Africa	*Dahlgren & Strid 2012*	LD	3	SEM	24A, B	Some tetracolporate
Endonema lateriflora (L. f.) Gilg.	South Africa	*Dahlgren & Strid 4979*	LD	3	SEM	25A–C	
Glischrocolla formosa (Thunb.) R. Dahlgren	South Africa	*Kerfoot 5723*	LD	5	SEM, TEM	23A, C, E, 27A	Some tetracolporate
Penaea cneorum Merrb. subsp. *cneorum*	South Africa	*Dahlgren & Strid 2982*	LD	4	SEM	23B, D, F	Tetracolporate
P. cneorum Meerb. subsp. *ruscifolia* R. Dahlgren	South Africa	*Dahlgren & Strid 2090*	LD	–	TEM	27F	
P. mucronata L.	South Africa	*Grant 2630*	MO	4	SEM, TEM	22A–C, 26A	Tetracolporate
Saltera sarcocolla (L.) Bullock	South Africa	*Dahlgren & Strid 3892*	LD	3	SEM, TEM	24C–E, 27C, D	Some 6-colporate
S. sarcocolla (L.) Bullock	South Africa	*Dahlgren & Strid 4988*	LD	–			
Sonderothamnus petraeus (Sond.) R. Dahlgren	South Africa	*Dahlgren & Strid 3654*	LD	3	SEM, TEM	25E, F, 26B, C	
S. speciosus (Sond.) R. Dahlgren	South Africa	*Dahlgren & Strid 3764*	LD	3	SEM, TEM	23G, 24F, 26D	Some tetracolporate

TABLE 1. Continued.

Taxon	Locality	Collector	Herbarium	Subsidiary Colpi	SEM-TEM	Figure No.	Remarks
Stylapterus ericoides A. Juss. subsp. *pallidus* R. Dahlgren	South Africa	*Dahlgren & Strid 3365*	LD	4	SEM, TEM	22D–F, 27E	Tetracolporate
CRYPTERONIACEAE							
Axinandra zeylanica Thw.	Ratnapura Distr., Sri Lanka	*Waas 1210*	MO				
A. zeylanica Thw.	Sri Lanka	*Gunatilleke & Gunatilleke 582*	MO	3	SEM, TEM	28B, D, 30C	
Crypteronia leptostachys	Philippines	*Ramos 1478*	MO		TEM	30A	
C. paniculata Bl.	Thailand	*Niyomdham s.n.*	MO	2	SEM, TEM	30B, 31B, D	Dicolporate syncolpate
C. sp.	Burma	*Dickason 6680*	MO	2	SEM	31A	Dicolporate syncolpate
Dactylocladus stenostachys Oliv.	North Borneo	*Hassan 732 (A)*	A	3	SEM	28E	Some tetracolporate
D. stenostachys Oliv.	Sarawak	*Chai 39708*	MO		TEM	29B	
D. stenostachys Oliv.	Sarawak	*SPH 3975*	MO	3	SEM, TEM	28A, F, 29C	Some tetracolporate
D. stenostachys Oliv.	Sarawak	*Chai 1982*	MO	3	SEM, TEM	28C, G, 29A	
MELASTOMATACEAE							
Acanthella sprucei Hook. f.	Amazonas, Venezuela	*Davidse 2793*	MO	3	SEM, TEM	33E, 38D	
Adelobotrys tessmannii Marhgraf	Huanuco, Peru	*Woytkowski 7850*	MO	(3)	SEM, TEM	34A–C, 39A, B	Some grains were cube shaped with 4 colpi and 8 subsidiary colpi on its edges
Allomorphia caudata (Diels) Li	Yunnan, China	*Henry 10761*	MO	(3)	SEM	34D	
Astronia cumingiana Vidal	Sarawak	*James et al. S.34401*	MO	(3)	SEM, TEM	34E, 39C	
Bredia hirsuta Bl.	Tokunoshima, Japan	*Iwatsuki 523*	MO	(3)	SEM, TEM	34F, 39F	
Comolia stenodon (Naud.) Triana	Brazil	*King & Almeda 8370*	CAS	3	SEM	36H	
Dissochaeta celebica Bl.	Johore, Malaya	*Anderson 2667*	MO	3	SEM, TEM	33F, 38B	
Dissotis brazzae Cogn.	Yala, Zaire	*Agnew & Musumba 8572*	MO	3	SEM, TEM	33C, D, 38C	
Marumia nervosa Bl.	Selangor, Malaya	*Ahmad S.A. 1080*	MO	3	SEM, TEM	33A, B, 38A	

TABLE 1. Continued.

Taxon	Locality	Collector	Herbarium	Subsidiary Colpi	SEM-TEM	Figure No.	Remarks
Memecylon normandii Jacques-Felix	Ghana	*Hall & Abbiw s.n.*	MO	3	SEM	31E	
Miconia alypifolia Naud.	Peru	*Ochoa 11675*	CAS	3	SEM	36A–C	Some 6-colporate with colpi and intercolpar concavities
M. caesia Cogn. & Gleason ex Gleason	Colombia	*Barclay et al. 3352*	US	3	SEM	36D	
M. hondurensis Donn. Sm.	Costa Rica	*Almeda & Nakar 4088*	CAS	3	SEM	35D, E	Some dicolporate, syncolpate with intercolpar concavities
M. melanotricha (Triana) Gl. var. *melanotricha*	Panama	*Wilbur & Luteyn 19393*	CAS	(3)	SEM	35A–C	
Mouriri cf. *glazioviana* Cogn.	Minas Gerais, Brazil	*Anderson 8895*	MO	3	SEM	31F	
Osbeckia polycephala Naud.	Matale Distr., Sri Lanka	*Lazarides 7219*	MO	3	SEM, TEM	32B, 37D, E	
Oxyspora paniculata DC.	Yunnan, China	*Henry 9010A*	MO	(3)	SEM	34G, H, 39D, E	
Tibouchina candolleana (DC.) Cogn.	Minas Gerais, Brazil	*Williams & Assis 8044*	OKL	3	TEM	37C	
T. urvilleana (DC.) Cogn.	Cult. UC-Berkeley; native, Brazil	*Schmid 1980-12*	MO	3	SEM	32C	
Tococa broadwayi Urban	Venezuela	*Steyermark 94999*	US	3	SEM	36F	
T. formicaria Mart.		*Ratter 3253*	CAS	0	SEM	36G	
T. spadiciflora Triana	Carretera, Colombia	*Forero et al. 5703*	MO	?	SEM, TEM	36E, 40A	Polyads
T. spadiciflora Triana	Colombia	*Archer 1976*	US	?	SEM	35F–I	
T. stephanotricha Naud.	Marischal Prov., Peru	*Schunke 8106*	MO	0	SEM, TEM	36E, 40B, C	Triporate
Trembleya phlogiformis DC.	Minas Gerais, Brazil	*Irwin et al. 19723*	MO	3	SEM, TEM	32A, 37B	
Tristemma littorale Benth.	Lagos State, Nigeria	*Brown 938a*	MO	3	SEM, TEM	32D, 37A	
Votomita monadelpha (Ducke) Morley	Brazil	*Ducke 18494*	K	4	SEM	32E, F	Tetracolporate
MYRTACEAE							
Acmena smithii (Poir.) Merrill & Perry	Victoria, Australia	*Beauglehole & Finck ACB 32281*	NSW	(3)	SEM	47B	

TABLE 1. Continued.

Taxon	Locality	Collector	Herbarium	Subsidiary Colpi	SEM-TEM	Figure No.	Remarks
Austromyrtus bidwillii (Benth.) Burret	New South Wales, Australia	*W. Bauerlen 584*	NSW	0	SEM	48F	
Baeckea virgata Andrews	Cult. UC-Berkeley; native, Australia, New Caledonia	*Schmid 1980-13*		0	SEM	44A	
Balaustion microphyllum C. A. Gardner	Western Australia	*A. M. Ashby 312*	NSW	0	SEM	44C	
Callistemon citrinus (Curtis) Stapf	Cult. UC-Berkeley; native, Australia	*Schmid 1980-11*	UC	(3)	SEM	43B, D	
C. teretifolius F. Muell.	Cult. UC-Berkeley; native, Australia	*Schmid 1978-198*	UC	(3)	SEM	43A, C	
Calothamnus validus S. L. Moore	Cult. UC-Berkeley; native, Australia	*Schmid 1980-14*	UC	(3)	SEM	43E	Some tetracolporate
Chamaelaucium uncinatum Schau.	Western Australia	*Webster 18570*	NSW	0	SEM	44F, H	Some dicolporate
Cleistocalyx operculata (Roxb.) Merrill & Perry	Darwin, Australia	*Byrnes 2786*	NSW	(3)?	SEM	47A	
Eremaea pauciflora Domin	Western Australia	*Coveny 8073*	NSW	0	SEM	43F	
Eucalyptus ficifolia F. Muell.	Cult. UC-Berkeley; native, Australia	*Schmid 1980-10*	UC	(3)	SEM	42C–E	
E. robusta Smith	Michoacan, Mexico	*Cutler 4044*	OKL	(3)	SEM	42F	
Eugenia capuli (Schl. & Cham.) Berg.	Cayo Distr., Belize	*Croat 23525*	OKL	0	SEM	47C	
E. elliptifolia Merrill	Leyte, Philippines	*Wenzel 1248*	MO	(3)	SEM	47D	
Heteropyxis natalensis Harv.	Natal, South Africa	*Davidson 2642*	MO	(3)	SEM	42A, B	
Homoranthus wilhelmii Cheel	Northern Eyre Peninsula, Australia	*Alcock 4038*	NSW	0	SEM	44B	
Hypocalymna angustifolium Schau.	Western Australia	*Coveny 8063*	NSW	0	SEM	44E, G	
Luma chequen (Molina) A. Gray	Cult. UC-Berkeley; native, Chile	*Schmid 1978-194A*	UC	0	SEM	47E	
Melaleuca decussata R. Brown	Cult. UC-Berkeley; native, Australia	*Schmid 1980-9*	UC	0	SEM	45C	

TABLE 1. Continued.

Taxon	Locality	Collector	Herbarium	Subsidiary Colpi	SEM-TEM	Figure No.	Remarks
M. hypericifolia Smith	Cult. UC-Berkeley; native, Australia	*Schmid 1978-195*	UC	(3)	SEM	45A, B	
M. preissiana Schau.	Cult. UC-Berkeley; native, Australia	*Schmid 1978-196*	UC	0	SEM	45D	
M. pulchella R. Brown	Cult. UC-Berkeley; native, Australia	*Schmid 1980-15*	UC	0	SEM	45G	Some tetracolporate
M. rhaphiophylla Schau.	Margaret River, West Australia	*Earle 70*	OKL	(3)	SEM	45E	
Metrosideros nervulosa C. Moore & F. Muell.	Lord Howe Is., Australia	s. col.	NSW 108602	(3)?	SEM	41B	
M. polymorpha Gaud.	Oahu, Hawaii, USA	*Chambers 3005*	OKL	(3)?	SEM	41A	
Myrceugenella apiculata DC.	Pucara Peninsula, Argentina	*Dawson & Schwabe 203A*	OKL	0	SEM	47F	
Myrtus communis L.	Cult. UC-Berkeley; native, Europe	*Schmid 1980-18*	UC	0	SEM, TEM	48B–D, 49A–D	Some tetrahedral tetrads
Osbornia octodonta F. Muell.	Idlers Bay, Papua New Guinea	*Womersley NGF 14065*	NSW	0	SEM	46G	
Pilidiostigma glabrum Burret	New South Wales, Australia	*Brown 1900*	NSW	0	SEM	46F	
Psidium littorale Raddi	Cult. UC-Berkeley; native, trop. America	*Schmid 1980-8*		0	SEM	46A–C	Some tetracolporate, some tetrahedral tetrads
Psiloxylon mauritianum Baill.	Mauritius	*Gueho s.n.*	MAU 14976	0	SEM	45F	Some tetracolporate
Rhodamnia argentea Benth.	New South Wales, Australia	*Maiden & Boorman s.n.*	NSW	0	SEM	48E	
Temu divaricatum Berg	Valdivia, Chile	*Buchtien s.n.*	NSW	0	SEM	48A	
Thryptomene calycina J. M. Black	Grampians, Victoria Australia	*Beauglehole ACB 28154*	NSW	0	SEM	44D	
Tristania conferta R. Brown	Cult. UC-Berkeley; native, Australia	*Schmid 1980-7*	UC	(3)	SEM	41C, D	
T. lactiflua F. Muell.	Western Distr., Papua New Guinea	*Henty & Foreman NGF 49383*	MO	(3)	SEM	41F	

TABLE 1. Continued.

Taxon	Locality	Collector	Herbarium	Subsidiary Colpi	SEM-TEM	Figure No.	Remarks
T. nereifolia R. Brown	New South Wales Australia	*Constable 5566*	K	0	SEM	41E	Triporate?
Ugni molinae Turcz	Cult. UC-Berkeley; native, Central and South America	*Schmid 1980-17*	UC	0	SEM	46D, E	Some di- or tetracolporate
ONAGRACEAE							
Boisduvalia densiflora (Lindl.) S. Wats.	Washington, USA	*Piper s.n.*	MO	0	SEM	58B, E	
B. densiflora (Lindl.) S. Wats.	Oregon, USA	*Thompson 5099*	MO	0	SEM	58C	
B. densiflora (Lindl.) S. Wats.	California, USA	*Abrams 6675*	DS	0	TEM	63C	
B. macrantha Heller	Oregon, USA	*Heller 12920*	MO	0	TEM	63A–C	
B. stricta (A. Gray) Greene	California, USA	*Jones s.n.*	MO	0	SEM	58A	
Calylophus berlandieri Spach subsp. *berlandieri*	Oklahoma, USA	*Towner 139*	DS	0	TEM	61E, F	
C. toumeyi (Small) Towner	Arizona, USA	*Towner 107*	DS	0	SEM	55A–D	
Camissonia arenaria (A. Nels.) Raven	California, USA	*Parish & Parish 254*	MO	0	SEM	57A, B	
C. arenaria (A. Nels.) Raven	Arizona, USA	*Nelson 10140a*	MO	0	SEM, TEM	57D, F, 61A	
C. cardiophylla (Torr.) Raven subsp. *cedrosensis* (Greene) Raven	Arroyo Malurino	*Moran & Reveal 19868*	MO?	0	SEM	57H	
C. robusta (Raven) Raven	California, USA	*Gould 978*	MO	0	SEM	57E, G	
C. tanacetifolia (Torr. & Gray) Raven subsp. *tanacetifolia*	Cult. UC-Berkeley; native, western NA	*UCB 69.1097*	UC	0	SEM	57C	
Circaea alpina L. subsp. *imaicola* (Ash. & Magn.) Kitamura	China, Xizang (Tibet)	*Monbeig s.n.*	MO	0	SEM	50D	
C. cordata Royle	Oslo, Norway	Cult. Missouri Bot. Gard.	MO	0	SEM	50C	

TABLE 1. Continued.

Taxon	Locality	Collector	Herbarium	Subsidiary Colpi	SEM-TEM	Figure No.	Remarks
C. mollis Sieb. & Zucc.	Kerita, Honshu, Japan	*Togasi 1797*	MO	0	TEM	60D, F	
Clarkia breweri Greene	California, USA	*Carter 1166*	LA	0	TEM	62D	
C. speciosa Lewis & Lewis subsp. *speciosa*	California, USA	*UCB 65.1421*	UC	0	SEM	52A, C	
C. unguiculata Lindl.	Cult. UC-Berkeley; native, western North America	*UCB 59.1244*	UC	0	SEM	52B, D, F	
Epilobium collinum C. C. Gmelin	Sortavala, Finland	*Lindberg s.n.*	MO	0	TEM	63G	
E. cylindricum D. Don.	Gulmarg, Kashmir	*Stewart 10353*	MO	0	TEM	63F	
E. glaberrimum Barbey	California, USA	*MacMillan 14618*	MO	0	SEM	59H	
E. hectorii Hausskn.	New Zealand	s. col.	CHR 202446	0	SEM	59I	
E. hirsutum L.	Pyrenees, France	*Gautier 489863*	DS	0	TEM	63D, E	
E. brachycarpum Presl	Oregon, USA	*Sheldon S11070*	MO	0	SEM	59A–D	
E. brachycarpum Presl	California, USA	*Greene, 1876*	MO	0	SEM	59E–G	
E. rigidum Hausskn.	Oregon, USA	*Kline M561*	MO	0	SEM	59I	
Fuchsia cylindracea Lindl.	Todos Santos, Mexico	*Linderman 2030*	MO	0	TEM	60A	
F. garleppiana Kuntze & Wittmark	Dept. Cochábamba, Boliva	*Melhus & Goodman 3618*	OKL	0	SEM	50B	
F. thymifolia HBK. subsp. *thymifolia*	Michoacan, Mexico	*Waterfall 16474*	OKL	0	SEM	50A	
Gaura calicola Raven & Greg.	Texas, USA	*Henrickson 11334*	US	0	SEM	53A	
G. coccinea Pursh	Texas, USA	*Reverchon 3844*		0	TEM	62A, B	
G. demareei Raven & Greg.	Arkansas, USA	*Demaree 62683*	US	0	SEM	53D	
G. lindheimeri Engelm. & Gray	Cult. UC-Los Angeles: native, central USA	*Raven*, 1971	LA	0	SEM	52E	
G. mutabilis Cav.	Chihuahua, Mexico	*Jones*, 1903	DS	0	SEM	52G, H	
G. neomexicana Wooton subsp. *neomexicana*	New Mexico, USA	*Towner 109*	US	0	SEM	53B, C	
Gayophytum micranthum Hook. & Arn.	Prov. Coquimbo, Chile	*Werdermann 200*	MO	0	SEM	53F, H	

TABLE 1. Continued.

Taxon	Locality	Collector	Herbarium	Subsidiary Colpi	SEM-TEM	Figure No.	Remarks
G. micranthum Hook. & Arn.	Prov. Coquimbo, Chile	*Moore 216*	LA	0	TEM	61D	
G. ramosissimum Torr. & Gray	Wyoming, USA	*Gooding 510*	MO	0	SEM	53E, G, I	
Gongylocarpus fruitculosus (Benth.) T. S. Brandegee subsp. *glaber* (J. H. Thomas) Carlquist & Raven	Baja California, Mexico	*Moran 3529*	DS	0	SEM	56F	
G. rubricaulis Schlecht. & Cham.	Mexico	*Davidse 9790*	MO	0	TEM	61G, H	
G. rubricaulis Schlecht. & Cham.	Veracruz, Mexico	*Sharp 44846*	MO	0	SEM	56D	
Hauya elegans DC. subsp. *barcenae* (Hemsl.) Breedlove & Raven	Chiapas, Mexico	*Breedlove 10229*	MO	0	SEM	50G	
H. elegans DC. subsp. *elegans*	San Luis Potosi, Mexico	*Moran 13387*	MO	0	SEM	50E	
H. elegans DC. subsp. *elegans*	Queretaro, Mexico	*Rzedowski 9294*	DS	0	SEM	50F	
H. heydeana Donn. Sm.	Chiapas, Mexico	*Breedlove 15653*	DS	0	TEM	60C, E	
Heterogaura heterandra (Torr.) Cov.	California, USA	*Raven 20238*	MO	0	SEM	54A–C	
H. heterandra (Torr.) Cov.	California, USA	*Bacigalupi 2341*	DS	0	TEM	62C	
Lopezia grandiflora Zucc.	Jalisco, Mexico	*Breedlove 8066*	DS	0	TEM	61B	
L. longifolia (Decne.) Plitmann, Raven & Breedlove	Morelos, Mexico	*Breedlove 8044*	DS	0	SEM	51D–G	
L. racemosa Cav. subsp. *racemosa*	Jalisco, Mexico	*Breedlove 25800*	CAS	0	SEM	51A–C	
Ludwigia alternifolia L.	North Carolina, USA	*Peng 3738*	MO	0	SEM	58F	
L. brevipes (Long) Eames	South Carolina, USA	*Godfrey & Tryon 1237*	MO	0	TEM	60B	
L. goiasensis T. P. Ramamoorthy	Brasilia, Brazil	*Ramamoorthy 652*			SEM	58D, G	

TABLE 1. Continued.

Taxon	Locality	Collector	Herbarium	Sub-sidiary Colpi	SEM-TEM	Figure No.	Remarks
L. longifolia (DC.) Hara	Tucuman, Argentina	*Venturi 2873*	MO	0	SEM	58H, I	
Oenothera brachycarpa A. Gray	Durango, Mexico	*Anderson 5207* Cult. Stanford Univ.	MO	0	SEM	56A, B	
O. maysillesii Munz	Durango, Mexico	*Breedlove s.n.*	MO	0	TEM	62E	
O. texensis Raven & Parnell	Texas, USA	*Parnell s.n.*	MO	0	SEM	56C, E	
Stenosiphon linifolius (Nutt.) Heynh.	Kansas, USA	*Raven 26384*	MO	0	SEM	55E, F	
S. linifolius (Nutt.) Heynh.	Kansas, USA	*Raven 26554*		0	TEM	62F	
Xylonagra arborea Donn. Smith & Rose subsp. *wigginsii* Munz	Baja California, Mexico	*Verity et al. 032*	MO	0	SEM, TEM	54D–F, 61C	

therefore, he recommends the term "subsidiary colpi" and we are in complete accord (Patel et al., 1983b). Subsidiary colpi generally have a thinner ektexine than the surrounding mesocolpial areas but in contrast to the colpi, all exine layers are usually represented. Frequently, the thinning of the ektexine is gradual and thus the subsidiary colpi often are not as clearly delimited as the colpi, although the endexine is increased in thickness just as in the colpi. Further, the surface sculpture in the subsidiary colpi is often different from that of the colpi. In the present study subsidiary colpi have been observed in Lythraceae, Combretaceae, Melastomataceae, Rhynchocalycaceae, Oliniaceae, Penaeaceae, and Crypteroniaceae, characterizing all pollen examined in the latter four families. Other families in which they have been observed are the Acanthaceae, Boraginaceae, Hydrophyllaceae, Leguminosae, and Verbenaceae (Erdtman, 1971; Nowicke & Skvarla, 1974; Faegri & Iversen, 1975; Ferguson & Skvarla, 1981, 1983; Raj, 1983). Subsidiary colpi are either equal to the number of colpi (= isomerous) and alternating with them or there can be additional subsidiary colpi, as particularly noted in the Lythraceae.

2. *Intercolpar concavities.* As originally defined by Wodehouse (1928: 453) for pollen in the Compositae tribe Mutisieae "These two species . . . are unique in the possession of three distinct concavities appearing as the impressions one could make with the thumb in a ball of soft dough. Since these impressions are between the furrows, I shall call them intercolpar concavities, and their position on the equator suggests the further designation of equatorial concavities." We consider them to be structurally and functionally similar to subsidiary colpi, distinguished only in that they are markedly larger. In this study intercolpar concavities are found in some Melastomataceae, Penaeaceae, and Myrtaceae. They may also be present in Lythraceae as they appear to be in light photomicrographs of *Peplis portula* by Guers (1970). In *Crypteronia* large concavities in the mesocolpia have been considered by Muller (1975) as pseudocolpoid depressions. Intercolpar concavities have also been described in Calyceraceae (Skvarla et al., 1977) and, if our interpretations of Erdtman (1971) and Raj (1983) are correct, perhaps in Hoplestigmataceae, Verbenaceae, and Olacaceae. Like subsidiary colpi, it will be of considerable interest to learn of their occurrence in other angiosperm groups.

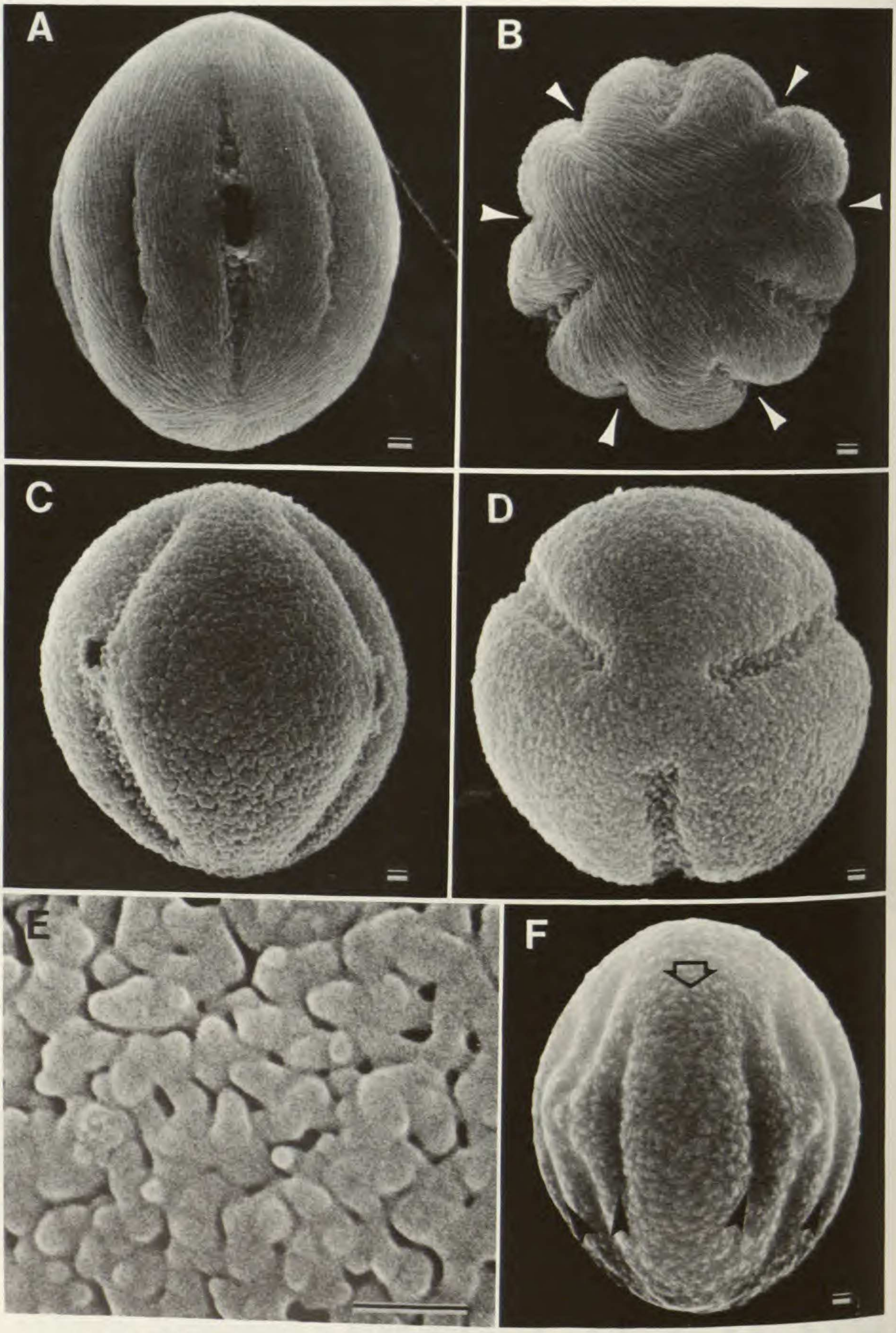

FIGURE 1. Scanning electron micrographs of Lythraceae subfam. Lythroideae pollen. A, B. *Nesaea schinzii*.—A. Lateral view showing granular colpus with circular endoaperture (at center) and two subsidiary colpi. The exine surface is striate.—B. Polar view. Each of the three colpi alternates with two subsidiary colpi (arrowheads). Note that *all* of the nine mesocolpia are equal in size. Comparison should be made with the scanning electron micrograph of *N. longipes* (Graham, 1977, figs. 4–6) in which the three mesocolpia that are flanked by subsidiary colpi are prominent and larger than the remaining six mesocolpia. C–E. *Heimia salicifolia* (*Ventura 2430*).—C. Lateral view.—D. Polar view.—E. Surface detail. The three colpi have a granular surface. Subsidiary colpi are absent. The mesocolpium consists of elongated, branched, often overlapping elements. Comparison with the scanning electron micrograph of Graham (1977, figs. 1–3) indicates a somewhat different sculptured surface.—F. *Crenea surinamensis*. Lateral view showing two shallow colpi and four subsidiary colpi (arrowheads). The

3. *Heterocolpate.* This term signifies the presence of subsidiary colpi or intercolpar concavities in addition to colpi and was originally defined by Faegri and Iversen (1950: 129) "Some furrows with, others without pores, free pores absent."

RESULTS AND DISCUSSION

LYTHRACEAE

Subfamily Lythroideae

Pollen is tricolporate (some heterocolpate with either three or six subsidiary colpi), radially symmetrical, and isopolar. Great variability exists in shape, surface sculpture, aperture system, and to a lesser extent, exine structure. Apart from *Nesaea* (Fig. 1A, B) and *Ammannia* (Fig. 2A, B) which are similar, each genus we examined has a distinct morphology and is described below.

Ammannia: A. robusta (Fig. 2A, B) is heterocolpate with six subsidiary colpi, subprolate in lateral view, circular in polar view. The surface is striate. Colpi are long with obtuse ends and with a smooth, slightly granular surface. The endoapertures are circular to slightly elliptic-lalongate. Subsidiary colpi are short with a slightly granular surface. *Ammannia coccinea,* which also has a striate surface and six subsidiary colpi, was examined along with *A. robusta* in TEM (Fig. 5A, B). The endexine is as thick or slightly thinner than the ektexine in the mesocolpial area. The foot layer is thick and often shows irregular channels near its lower margin, columellae are thick, short, and simple and the tectum is very thin and imperforate. In cross section, the striae composing the tectum appear deeply grooved and constricted at the base. In the colpal and subsidiary colpal regions, the endexine is as thick or slightly thicker than in mesocolpial regions and the foot layer appears to be continuous as a very thin film. Near the endoaperture, the endexine is granular and continues as a very thin layer over the pore.

Crenea: C. surinamensis (Fig. 1F) was examined only with SEM. The pollen is spheroidal to subprolate in lateral view, while in polar view the slightly collapsed grains are triangular with meridional ridges forming obtuse corners. Pollen is heterocolpate with six subsidiary colpi, the mesocolpia between each pair of subsidiary colpi are wide and thick, forming three meridional ridges. Colpi are long and indistinct; subsidiary colpi are shorter than the colpi and also indistinct. Endoapertures are circular and raised. The surface is verrucate-rugulate.

Cuphea: Both *C. carthagenensis* (Fig. 2C) and *C. petiolata* (Fig. 2D–F) are tricolporate-syncolpate, oblate-suboblate in lateral view, triangular (sub-triangular to circular in *C. petiolata*) in polar view, and goniotreme (i.e., angulaperturate). In *C. carthagenensis,* the surface is psilate with meridional folds or ridges on the mesocolpia toward the pores. Colpi are very narrow and united at the poles. The pores are aspidote, like a cylindrical extension, and open by a vertical splitting of the cylinder. In *C. petiolata,* the corners are obtuse, the surface is basically striate, but on the equator on each side of the colpus two elliptic areas are delineated in some grains. The size and the sculpture of these areas are highly variable and range from striate-spinulate to rugulate-striate in grains from the same collection. Colpi have a granular surface and the endoapertures are lalongate.

Cuphea nitidula (Fig. 5D) and *C. racemosa* (Fig. 5C) were examined with TEM. The former is oblate-triangular with protruding pores (SEM not included here). It has a uniform endexine which is thickened at the base of the pores. The foot layer is thin, columellae are simple and extremely short. The tectum is thin and tectal perforations are rare. Tectal ridges are solid. The protruding pore (not illustrated in plate figures) has a thin granular endexine, a fragmented and thin foot layer, short columellae, and a very thin but continuous tectum. *Cuphea racemosa* has suboblate, tricolporate grains (Cos Campos, 1964). In thin section (Fig. 5C), the endexine is thin and uneven, the foot layer is thick, columellae are short, and the tectum is thin with some perforations. However, the endexine is very thick below the colpi and granular near the endoapertures (not illustrated).

Diplusodon: D. villosus was examined with SEM and TEM (Figs. 3A, B, 6E). The tricolpoi-

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mesocolpium (open arrow) between the subsidiary colpi is wide and forms a meridional ridge. The exine surface is verrucate-rugulate. This pollen grain (see also scanning electron micrograph of Muller, 1981, Pl. 1, figs. 1, 2) is in marked contrast to other grains with six subsidiary colpi (viz. Figs. 1A, B, 2A) in that adjacent colpi and subsidiary colpi are not all equidistant. Scales equal 1 μm.

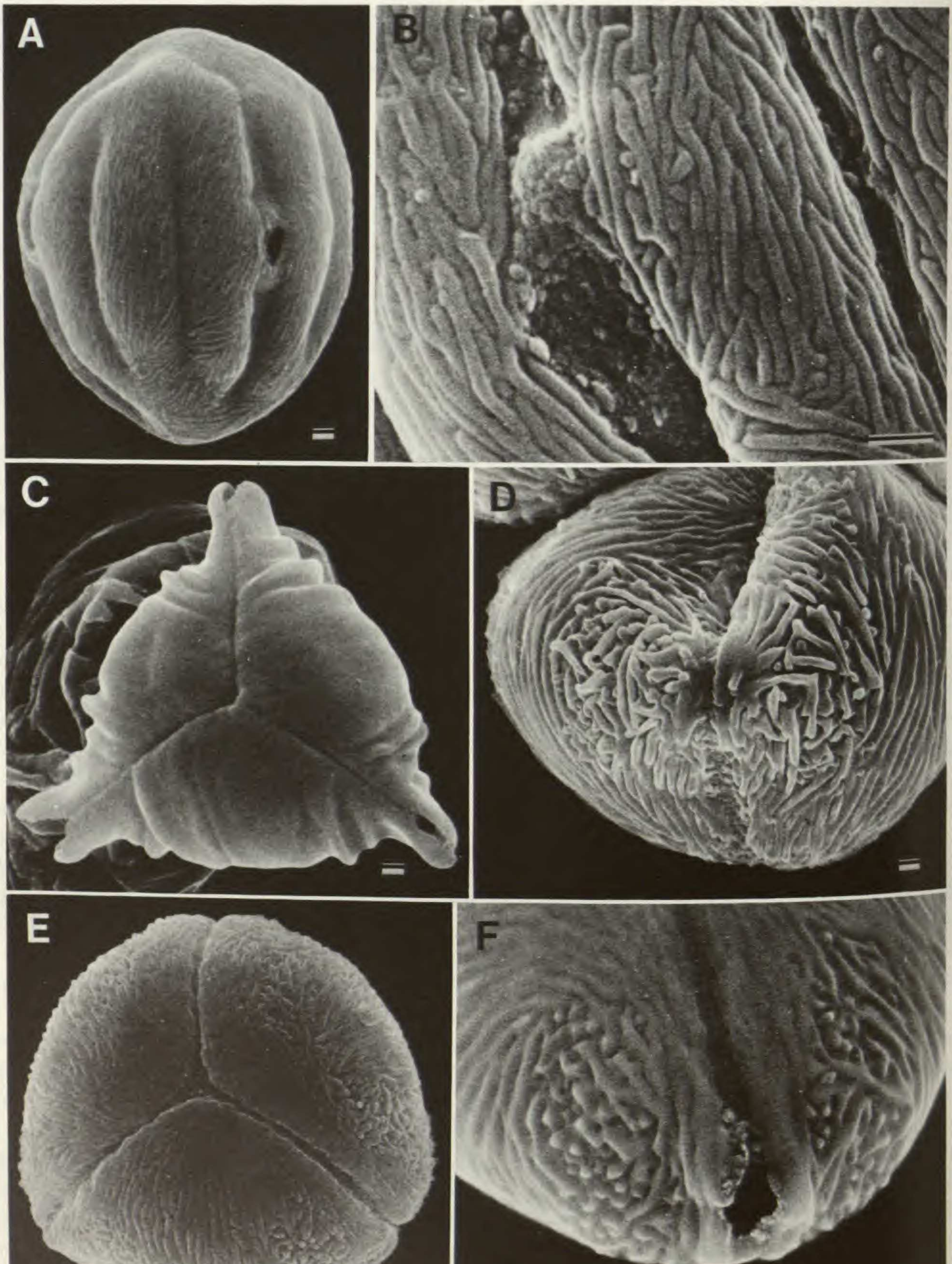


FIGURE 2. Scanning electron micrographs of Lythraceae subfam. Lythroideae pollen. A, B. *Ammannia robusta.*—A. Lateral view. Each colpus is separated by two subsidiary colpi. The exine surface is striate.—B. Surface detail near the endoaperture which is covered by a granular colpus membrane.—C. *Cuphea carthagenensis.* Polar view. Pores are located in the cylindrical extensions on the three corners; colpi are narrow and united at the pole. The surface is psilate with large ridges (see transmission electron micrograph of *C. nitidula,* Fig. 5D) near the pores. D–F. *Cuphea petiolata.*—D. Lateral view with randomly oriented striae in the aperture region.—E. Polar view showing syncolpate apertures.—F. View of open endoaperture and surrounding striate surface. See also transmission electron micrograph surface replicas of other species of *Cuphea* (Graham et al., 1968, figs. 4, 5, 8). Scales equal 1 μm.

dorate grains are subprolate in lateral view. Endoapertures are circular. The surface is verrucate-rugulate with tightly packed verrucae as well as with elongated, convoluted rugulate elements. Colpi are very short and have large spherical elements on the surface. In section, the verrucate-rugulate surface elements appear to be composed of a thick tectum which is supported by several thin columellae. A foot layer is absent. The endexine is thick and uniform, near the pore it increases in thickness and is granular.

Heimia: H. salicifolia was examined with both SEM and TEM. Tricolporate pollen grains are spheroidal in lateral view and circular in polar view (Fig. 1C–E). The surface has irregularly shaped elements with overlapping fingerlike branches and irregular gaps between them (Fig. 1E). Blunt spinules are also scattered on the surface. Colpi are long, with obtuse ends and a granular surface. Endoapertures are lalongate. Thin section (Fig. 5G) shows a thick endexine, a foot layer which is either as thick as or thinner than the endexine, and simple or branched columellae which are erect and tall but becoming shorter toward the colpi. The lower margin of the tectum is more or less straight while the upper margin is irregular. Tectal perforations are numerous and often large. The endexine is very thick below the colpi; near the endoaperture, its lower margin is granular. The membrane over the endoaperture consists of very thin granular endexine. The granules on the colpi surface (not illustrated in plate figures) appear to be solid and constricted at the base or rarely with fine columellae under them.

Lafoënsia: L. punicifolia was examined with both SEM (Fig. 3D–F) and TEM (Figs. 5E–F, 6A). The tricolpoidorate grains are subprolate in lateral view, and triangular-pleurotreme with obtuse corners and straight sides in polar view. The three protruding pores are situated midway between the sides of the triangular pollen grain. The three meridional ridges and the polar caps separate three elliptic, apertural fields (Muller, 1981). The surface of the apertural fields is granular-verrucate-rugulate; the surface of the ridges and the margins of the apertural fields near the apocolpia are rugulate but coarser than the rest of the apertural fields. The apocolpia have a psilate surface. The short colpus appears as a slightly depressed area with fewer and smaller granular elements than the surrounding area. The pores are circular, the membrane over them is similar to and continuous with the surrounding area. In TEM (Figs. 5E, F, 6A) the ektexine is thick in the ridge areas and thin in the apertural fields and at the poles. In the ridge areas, the foot layer is thick, with the upper margin often irregular or raised into domes, columellae are tall, erect and simple, and the tectum is thick, but discontinuous due to the rugulate surface. In the apertural fields (Fig. 6A), the columellae are shorter, the foot layer is thinner, and the tectum irregular in thickness and discontinuous but with tightly packed verrucate units. The endexine in the ridge and aperture fields is thick and uniform (Figs. 5E, 6A). At the poles (Figs. 5F, 6A) the entire exine is thinner. Here the endexine is very thin, and the foot layer and tectum are thicker than the endexine. The tectum is continuous and has a smooth upper margin and an irregular lower margin; the very short columellae are wider at their distal ends and appear to be finely branched (Fig. 5F).

Lagerstroemia: L. speciosa was examined only with SEM. Tricolporate grains are subprolate in lateral view and circular to hexagonal in polar view (Fig. 3C). The surface appears to be microrugulate with cylindrical, often branched and overlapping irregularly compacted elements. On the mesocolpia, a poorly developed meridional ridge with two slightly depressed parallel areas on each side is discernible. Colpi are long with obtuse ends and a granular surface. Endoapertures are circular with a slightly raised membrane over them.

Nesaea: N. schinzii was examined only with SEM (Fig. 1A, B). The tricolporate grains are heterocolpate with six subsidiary colpi. They are subprolate in lateral view and circular in polar view. The surface is striate. Colpi are long with acute ends and a granular surface. Subsidiary colpi are shorter than the colpi and have a granular surface.

Subfamily Punicoideae

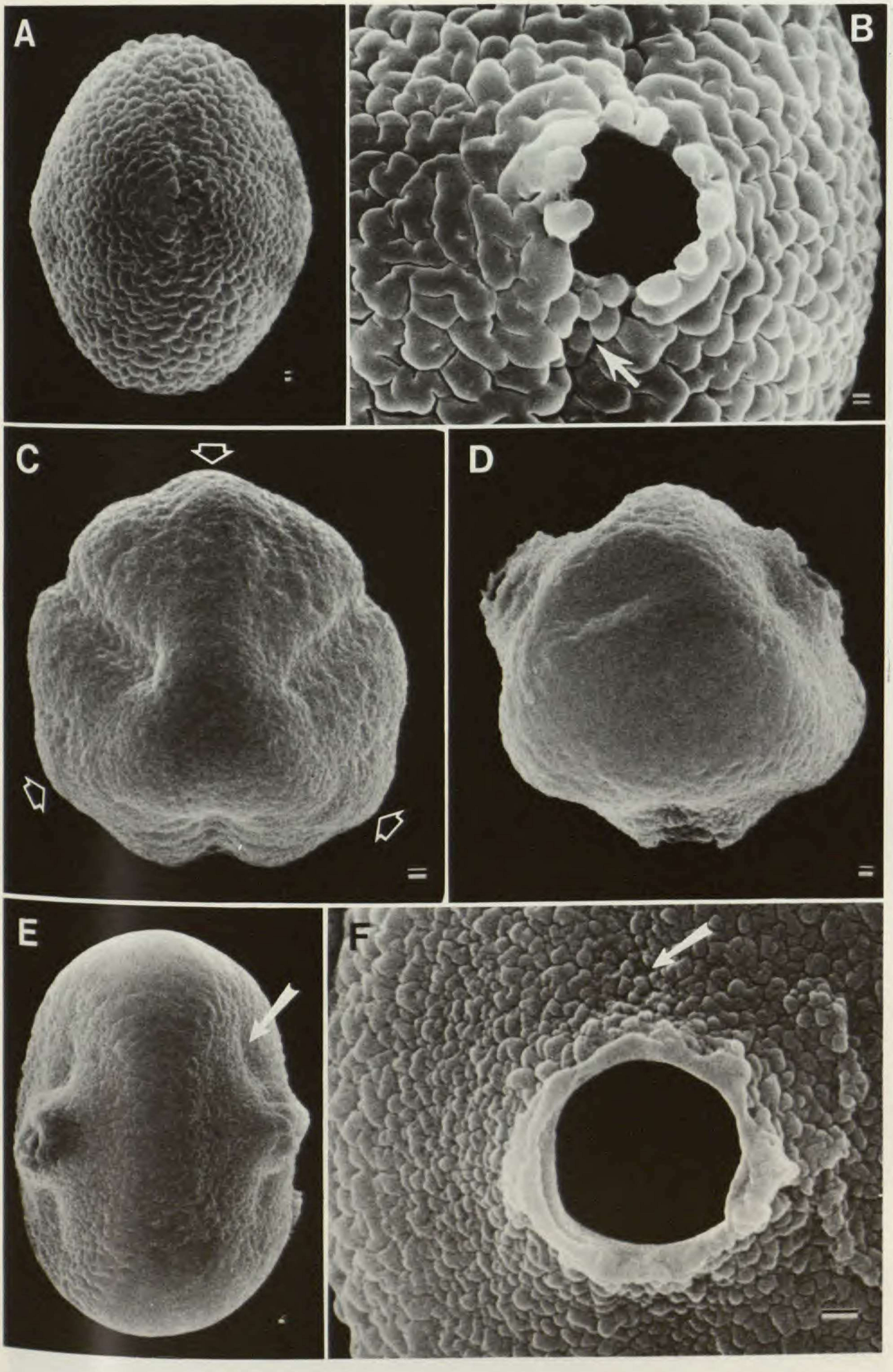
Punica protopunica and *P. granatum,* the only two species in the subfamily, were examined with SEM and TEM (Figs. 7, 8). The pollen is tricolporate, radially symmetrical, isopolar, subprolate in lateral view, and circular in polar view with slightly angular mesocolpia. In *P. protopunica* the meridional ridges, polar caps, and ovoid apertural fields are weakly developed (Fig. 7D). The surface of the polar caps is smooth-punctate with fine channels, that of the meridional ridges is coarsely rugulate. In the apertural fields, two faint subsidiary colpi with a rugulate surface (Fig. 7E) are present on the sides of each meridional ridge. In *P. granatum* only three weakly developed meridional ridges with rugulate surfaces were clearly observed in the center of the mesocolpia (Fig. 7A). Exclusive of ridges, the surface is granular-rugulate (Fig. 7B). In both species, colpi are long, with acute ends and with a granular surface. Endoapertures appear to be circular to slightly oblong and lalongate.

Thin sections show that the foot layer is narrow and discontinuous (Fig. 8A, B), although in the polar caps of *P. protopunica* it is continuous (Fig. 8C). The columellae are very short, thick, and numerous. They are branched where the exine is most thickened. The tectum is thick. The prominent endexine increases in thickness in the colpal regions and decreases at the polar caps. Near the endoapertures the endexine is granular. Punicoideae pollen is comparable to some Lythroideae although apertural fields, meridional ridges and polar caps are not as well developed.

FIGURE 3. Scanning electron micrographs of Lythraceae subfam. Lythroideae pollen. A, B. *Diplusodon villosus.*—A. Lateral view. The aperture system consists of a short colpus and circular endoaperture.—B. A verrucate-rugulate surface encompasses the short colpus (arrow) and prominent circular endoaperture.—C. *Lagerstroemia speciosa.* Polar view showing weakly developed meridional ridges (arrows) between each colpus. This scanning electron micrograph complements the one of Muller (1981, Pl. 1, figs. 3, 4) for the same species. D–F. *Lafoënsia punicifolia.*—D. Polar view showing prominently psilate polar cap, three protruding apertures, and three meridional ridges.—E. Lateral view with meridional ridge separating two apertural fields. Arrow indicates colpus.—F. The surface of the aperture field surrounding the pore is verrucate-rugulate. A portion of the colpus is indicated by an arrow. These scanning electron micrographs should be compared with those of Muller (1981, Pl. 7, figs. 1, 2). Scales equal 1 μm.

FIGURE 4. Scanning electron micrographs of pollen from Rhynchocalycaceae (A, C), Alzateaceae (B, D), and Lythraceae subfams. Sonneratioideae (E) and Duabangoideae (F). A, C. *Rhynchocalyx lawsonioides.*—A. Lateral view.—C. Polar view. Subsidiary colpi appear to be united (i.e., they are "synpseudocolpate") (arrow) at the pole. See also scanning electron micrograph of Muller (1975, Pl. V, figs. 7–11). B, D. *Alzatea verticillata.*—B. Polar view.—D. Lateral view. For both figures, the surface is psilate but at the middle of the mesocolpia slightly depressed psilate-punctate areas are noted (open arrows). These have been interpreted as incipient pseudocolpi (see scanning electron micrograph of Muller, 1975, Pl. IV, figs. 6–9). A distinct margin (solid arrow) is present around the colpus.—E. *Sonneratia caseolaris.* Sublateral view. Polar cap has a psilate surface with a few punctae. The well-developed meridional ridge has a rugulate surface. Note the two elliptic apertural fields and the protruding pores which are enclosed by two small ridges (arrowheads). The surface of the apertural fields and the membranes over the pores is verrucate. (See also scanning electron micrograph of Muller, 1978a, several plates.)—F. *Duabanga moluccana.* Lateral view. The surface is smooth on the polar caps; elsewhere it is verrucate-rugulate. The meridional ridge has a coarser surface than the apertural fields. In contrast to *S. caseolaris* (E) polar caps and meridional ridges are less distinct and the protruding pores are without surrounding ridges. Scales equal 1 μm.

FIGURE 5. Transmission electron micrographs of Lythraceae subfam. Lythroideae pollen.—A. *Ammannia robusta.* Cross section of the area between two colpi (short arrows) which includes three mesocolpia and two subsidiary colpi (long arrows). Note the distinct "white line" between the foot layer and endexine. The latter is granular on the right indicating the presence of an endoaperture.—B. *Ammannia coccinea.* Section of a mesocolpium. The striae are cut perpendicularly, are deeply lobed, and are constricted at their bases. The tectum (arrow) is very thin, columellae are short and thick; the foot layer is highly irregular and has some lamellae. The endexine is as thick as the entire ektexine.—C. *Cuphea racemosa.* Portion of a mesocolpium. Note thin, irregular endexine.—D. *Cuphea nitidula.* Section of the mesocolpium near pore (to the right but not included). The ridges (r) (as described in scanning electron micrograph Fig. 2C) are solid, columellae (arrow) are short and the foot layer is essentially uniform. The endexine increases in thickness toward the pore and is stained darker than the ektexine. E, F. *Lafoensia punicifolia.*—E. Section perpendicular to mesocolpium and including adjacent pores. The ektexine on the meridional ridge (within arrows) is more prominently developed than on the adjacent apertural fields. The endexine is well developed: under the meridional ridge it is nearly equal in thickness to the ektexine, toward the pores it becomes granular as well as increasing in thickness. This transverse section is in contrast to Figure 6A which represents a section parallel to the polar axis (i.e., a longitudinal section) and includes part of the polar cap and apertural field. These two different sectioning planes represented in E and Figure 6A explain the disparity in respective endexine thicknesses. See also Muller (1981, Pl. IV) for additional transmission electron micrographs.—F. Section of polar cap. In contrast to E and Figure 6A note particularly the smooth, solid tectum, and the thick and branched columellae. The uniform foot layer is thicker than the narrow endexine. This section is directly comparable to the transmission electron micrograph of Muller (1981, Pl. IX, fig. 3).—G. *Heimia salicifolia* (*Graham 141*). Section of a mesocolpium. Scales equal 1 μm.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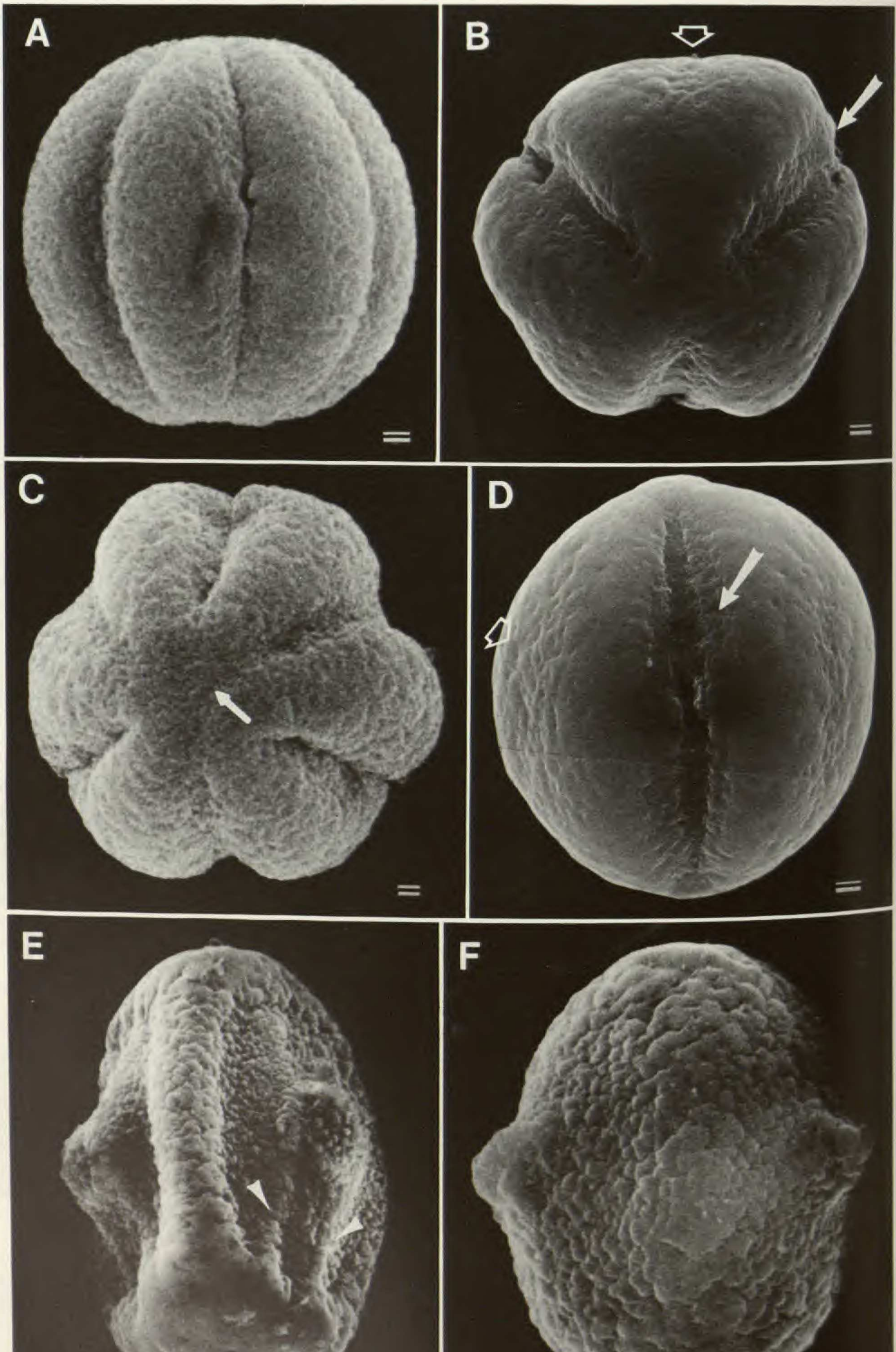
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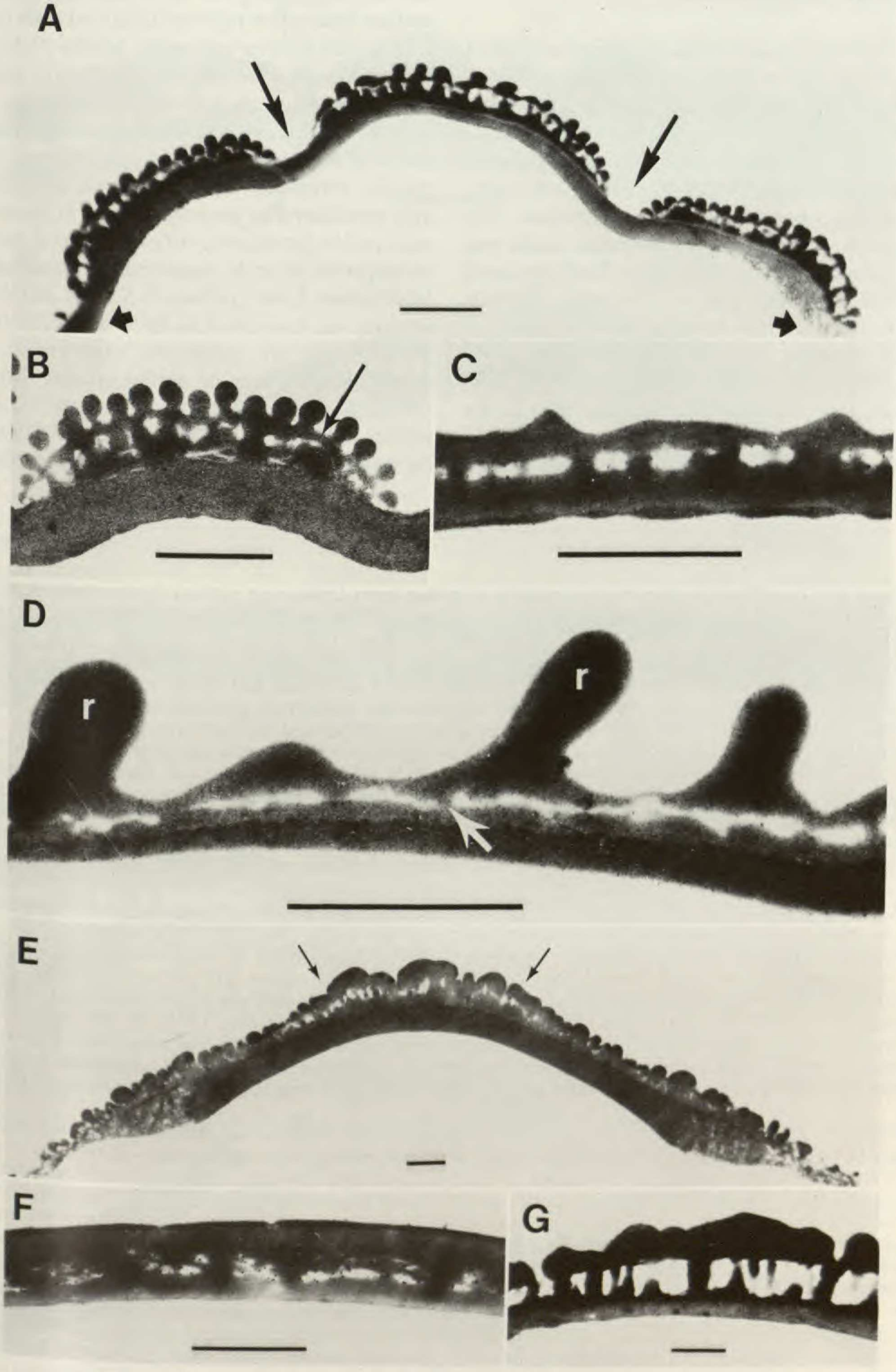
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Subfamily Sonneratioideae

Sonneratia caseolaris was examined with SEM (Fig. 4E, F). The pollen is triporate, radially symmetrical, and isopolar. *Sonneratia* grains are prolate, cylindrical in lateral view, and triangular-hexagonal in polar view, and three well-developed, meridional ridges alternating with three, oblong apertural (pore) fields are present. The surface is verrucate in the apertural fields and verrucate-rugulate on the ridges. Each apertural field has a protruding pore at its center. The surface of the pore membrane is similar to that of the surrounding field. In addition to the three large ridges, six smaller ridges are present, two in each apertural field. They are parallel to the larger ridges and have a rugulate surface. The pore is located between the two smaller ridges, and the large, triangular polar caps have a psilate surface with a few punctae scattered over them.

In a light microscope study, Muller (1969) described the pollen morphology for five species and two interspecific hybrids of *Sonneratia.* Major conclusions from his study were: (1) that *S. alba* and *S. caseolaris* pollen showed great intraspecific variability that is geographically related and considered as genotypic, and (2) the dominant pollen morphology of one parent of the two intraspecific hybrids suggested introgressive hybridization. Later, pollen of *S. alba* and *S. caseolaris* was examined by SEM and TEM (Muller, 1978a) in order to supplement the morphological data of earlier studies (Muller, 1969). Since our study did not include TEM observations, the pollen ultrastructure of *Sonneratia* is summarized from Muller's work as follows:

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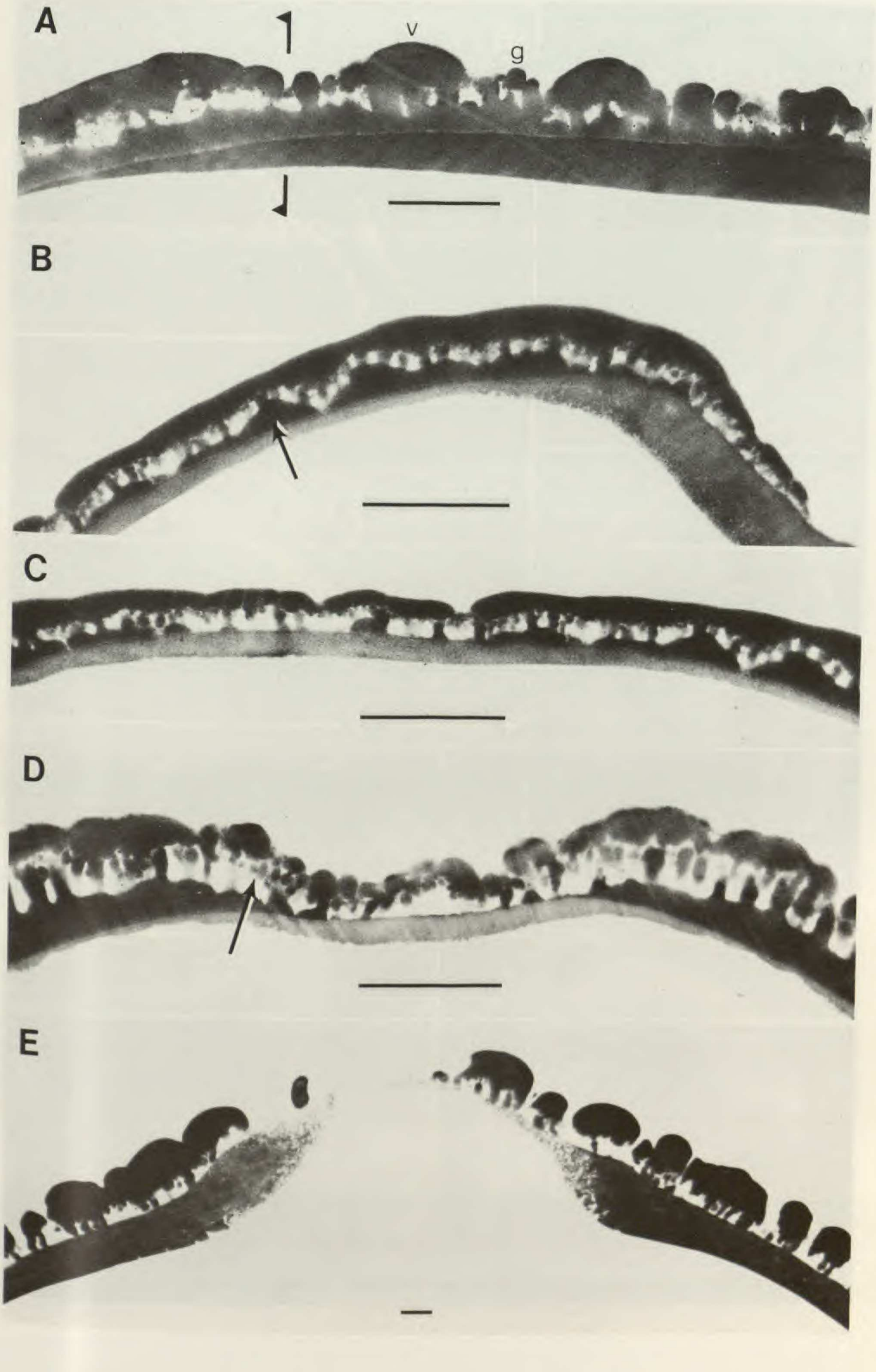
FIGURE 6. Transmission electron micrographs of pollen from Lythraceae subfam. Lythroideae (A, E), Alzateaceae (B, C), and Rhynchocalycaceae (D).—A. *Lafoënsia punicifolia.* Section through the polar cap (left of "bracket") and apertural field. In the apertural field, the verrucae (v) are composed of a thick tectum and short, perpendicular columellae. Between the verrucae the surface granules (g) of the scanning electron micrograph (Fig. 3D–F) are supported by columellae. The foot layer is well developed and has an irregular upper margin. The endexine is thick and more densely stained than the ektexine. Toward the polar cap the tectum is continuous and has a finely granular layer below it. The columellae are shorter and the foot layer is thicker than in the apertural field. The endexine decreases in thickness from right to left (i.e., toward the polar cap). (See additional comments to Fig. 5E, F and also Muller, 1981, Pl. IV.) B, C. *Alzatea verticillata.*—B. Section of a portion of the mesocolpium. At the extreme right is the colpus. The foot layer is highly irregular and forms "hills" (double arrow) and "valleys." The thickness and shape of the tectum is in direct correspondence with that of the foot layer, between them is a more or less uniform, columellae layer. Near the colpus, the tectum is thin, the columellae are short, and the foot layer is extremely thin. The endexine, which is relatively thin in the mesocolpium, is very thick in the colpus.—C. A continuation of the section in B to show the middle portion of the mesocolpium. Here, the entire exine decreases in thickness. The tectum is thinner than the surrounding areas and more perforate. The columellae either remain the same or slightly increase in length and are branched near the base of the tectum. The foot layer is either absent or present only as thickened bases of columellae. The endexine has increased in thickness, although considerably less so than in the colpus region.—D. *Rhynchocalyx lawsonioides.* The section is near the end of a colpus or subsidiary colpus and includes portions of two mesocolpia. The arrow indicates granules at the inner (lower) margin of the tectum (see also Muller, 1975, Pl. VII, figs. 1–3).—E. *Diplusodon villosus.* Section passing through a pore and including parts of the adjacent mesocolpia. The verrucae forming the surface sculpture are composed of a thick tectum supported by several thin columellae. A foot layer appears to be absent. The endexine is thick and uniform; in the pore area it is granular. Scales equal 1 μm.

FIGURE 7. Scanning electron micrographs of Lythraceae subfam. Punicoideae pollen. A, B. *Punica granatum* (*Grant 15704*).—A. Lateral view. A wide meridional ridge (between arrows) is discernible.—B. Granular-rugulate surface of mesocolpia near a part of a colpus. C–G. *Punica protopunica.*—C. Scanning electron micrograph of a fractured exine near the pole. Note the inner surface which is smooth toward the pole. The granules below the tectum (arrow) were not observed in sections.—D. Lateral view. A distinct meridional ridge is present, and is connected with the polar caps forming weakly developed apertural fields similar to those found in Lythraceae (Muller, 1981). Slightly coarser, elongated areas lateral to the ridge and suggesting subsidiary colpi are also distinct.—E. Lateral view showing the rugulate surface of the ridge (center) and the subsidiary colpi.—F. Polar view. Compare with Figure 3C.—G. Inner surface of the exine near the endoaperture. Scales equal 1 μm.

FIGURE 8. Transmission electron micrographs of Lythraceae subfam. Punicoideae pollen.—A. *Punica granatum* (*Grant 15704*). Transverse section of a mesocolpium. B, C. *Punica protopunica.*—B. Transverse section of a mesocolpium. Note the "white line" separating the discontinuous foot layer and the thick endexine.—C. A vertical section passing through an open pore. Note the thinning of the endexine at the poles (arrows). In contrast to other areas, the foot layer at the poles is thick and continuous. Scales equal 1 μm.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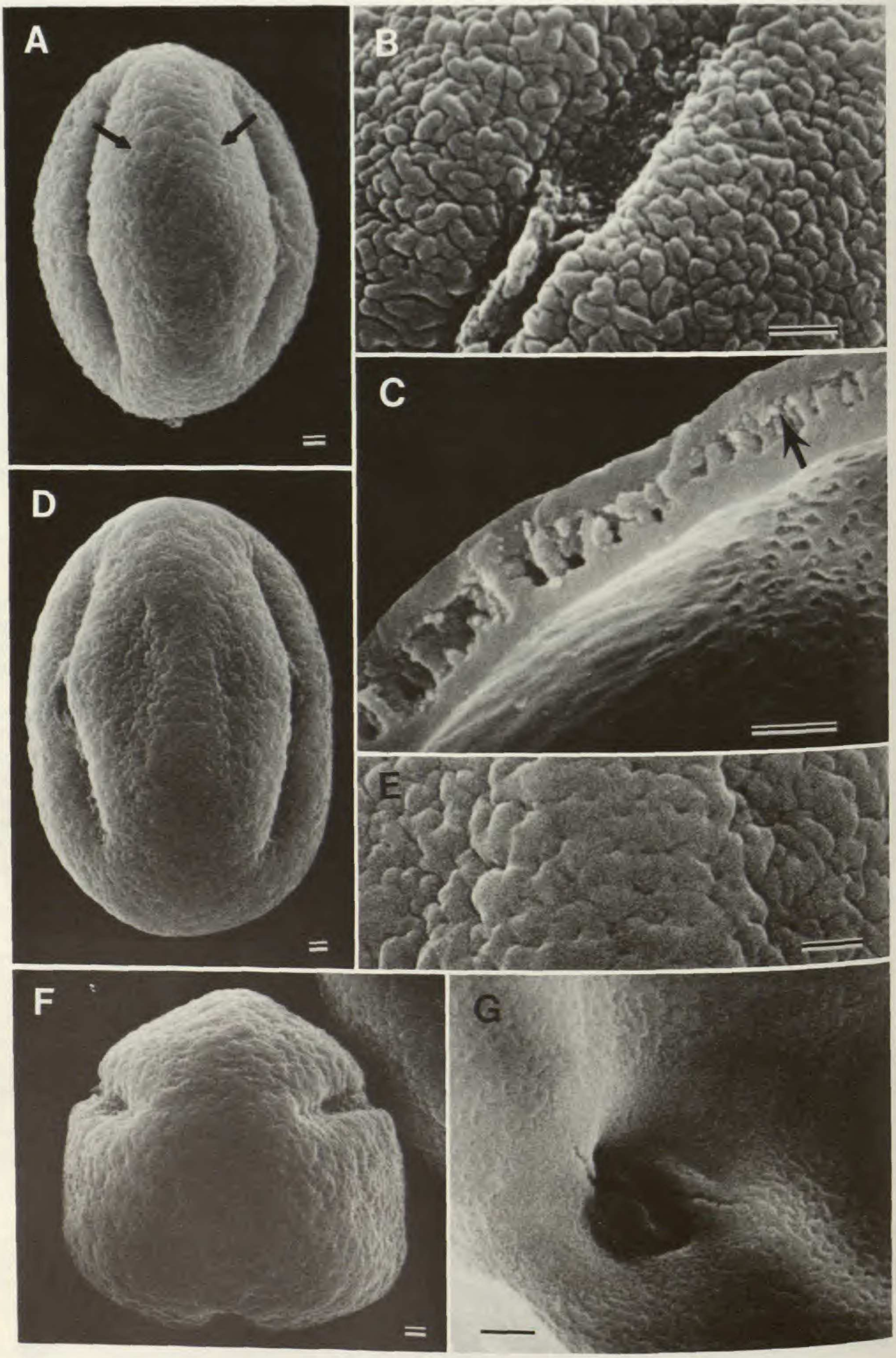
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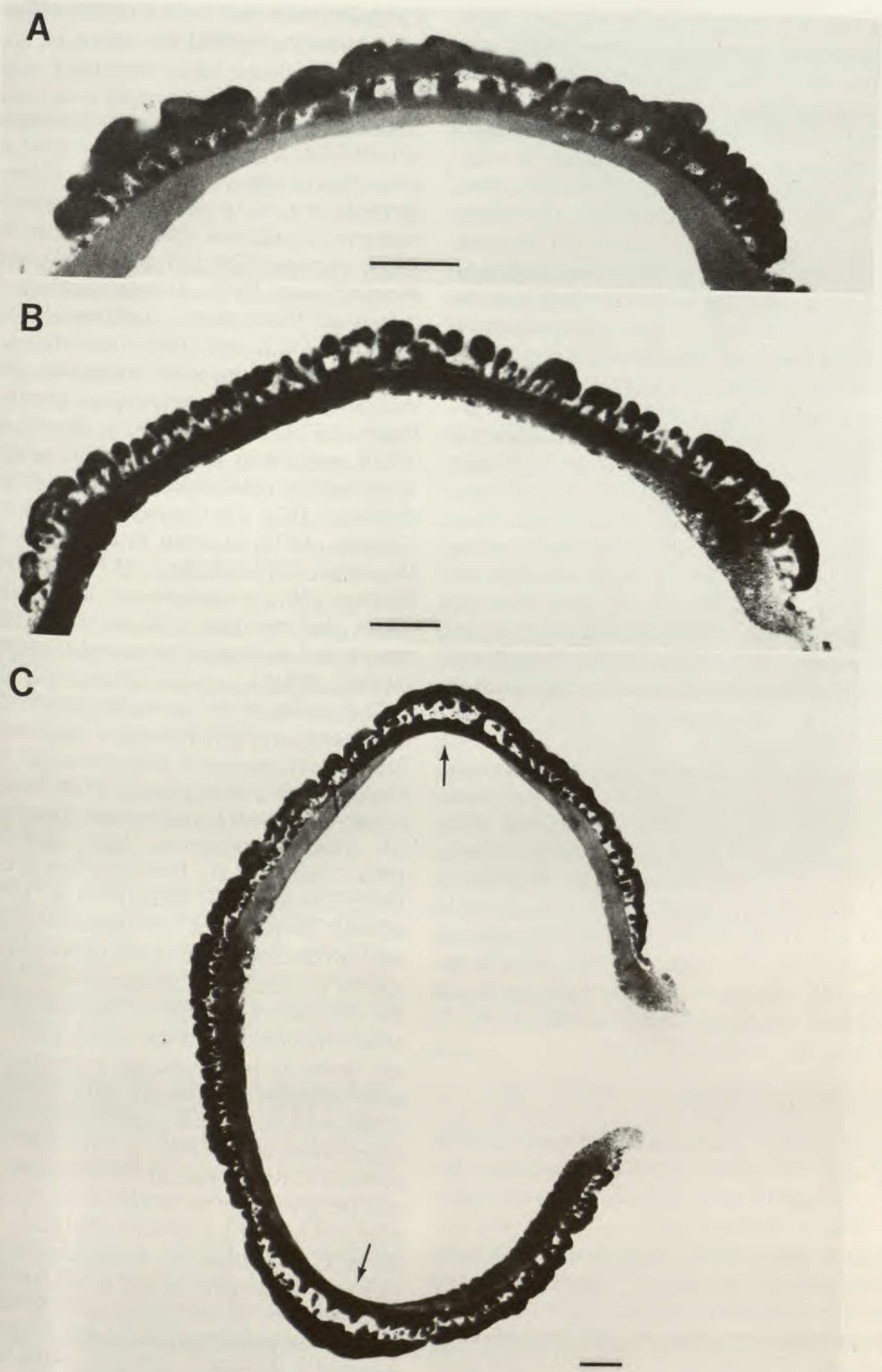
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the endexine is thin on the polar caps and thick in the equatorial zone. It is granular around the pores. The sole (= foot layer) on the other hand, is thick on the polar caps and thinner in the equatorial zone. In the porate fields of the equatorial zone, short columellae connect the verrucae to the sole. In the meridional ridge areas in *S. alba,* the columellae are longer and rather widely spaced, and support a tectum. At the polar caps, distinct columellae grade into areolate protrusions of the sole. The tectum is continuous on the polar caps, partially broken on the ridges (in *S. alba*) and occurs as separate verrucae over the porate fields. A granulate layer completely or partially fills the infractectal cavities. Muller emphasized that in *S. alba* well formed meridional ridges united with polar caps which markedly delineated apertural or porate fields, while in some grains of *S. caseolaris* the lack of meridional ridges did not confine the pores to fields, and in other grains, indistinct meridional ridges were found. The conclusion was that pollen of *S. alba* was more advanced in ". . . controlled harmomegathy than that of *S. caseolaris* and it is significant in this connection that the latter species has been proven to be phylogenetically older" (Muller, 1978a: 287–289).

Recognizing the taxonomic problems associated with distinguishing pollen of *S. caseolaris* from *S. alba* (Muller, 1969, 1978a), our SEM results show that at least superficially, *S. caseolaris* (Fig. 4E) appears more similar to Muller's SEM of *S. alba* (Muller, 1978a, Pl. II, fig. 1, 1981, Pl. VI, fig. 2) than to his SEM of *S. caseolaris* (Muller, 1978a, Pl. 1, figs. 1, 2, 1981, Pl. VII, fig. 3). The similarity is seen in the well-developed meridional ridges and apertural fields in our *S. caseolaris* and Muller's *S. alba.*

Subfamily Duabangoideae

Duabanga molucanna was examined with SEM (Fig. 4F). The pollen is triporate, radially symmetrical, and isopolar, and the shape is subprolate, elliptic in lateral view, and triangular-hexagonal in polar view. As in *Sonneratia,* three well-developed, meridional ridges alternating with three, oblong apertural (pore) fields are present, although the ridges are less pronounced in *Duabanga.* The surface is verrucate in the apertural fields and verrucate-rugulate on the ridges. Each apertural field has a protruding pore at its center. The surface of the pore membrane is similar to that of the surrounding field. The large, triangular polar caps have a psilate surface with a few punctae scattered over them.

Discussion

This report is in agreement with others which indicate that Lythraceae have the most diverse pollen morphology of the Myrtales. Much of this diversity centers on the apertural systems, for example, tricolporate grains are documented in *Physocalymma* (Cos Campos, 1964), *Pemphis, Rotala* (Guers, 1970), *Heimia* (Graham, 1977), *Adenaria, Pleurophora, Galpinia, Woodfordia* (Erdtman, 1971), and *Diplusodon* (Muller, 1981); heterocolpate grains with isomerous subsidiary colpi are present in *Lythrum* (Cos Campos, 1964; Guers, 1970; Heusser, 1971), *Rotala* (Guers, 1970), and *Peplis* (Heusser, 1971); grains with six subsidiary colpi occur in *Nesaea, Ammannia* (Erdtman, 1971; Cos Campos, 1964; Guers, 1970; Graham, 1977; Lobreau et al., 1969), *Crenea* (Erdtman, 1971; Muller, 1981), and *Lawsonia* (Muller, 1981), and grains with three meridional ridges that alternate with apertural fields are present in *Lafoënsia, Crenea,* and *Lagerstroemia* (Muller, 1981).

This pollen diversity is also common at the infrageneric level; for example, *Cuphea,* with over 250 species, shows a wide variation in morphology with pollen ranging from basic tricolporate-spheroidal to tricolporate-syncolpate-oblate triangular (Erdtman, 1971; Cos Campos, 1964; Graham et al., 1968; Graham & Graham, 1971; Guers, 1970. Graham et al. (1968) examined the pollen of 153 species of *Cuphea* in order to determine the extent of diversity among species as well as the potential use of pollen in the systematics of the genus. Starting with a basic oblate, tricolporate, striate, tectate grain, *Cuphea* was shown to be remarkably eurypalynous with great variation at sectional, subsectional, specific, and varietal levels. Twelve morphological categories representing eight sections and nine subsections were established. Of particular concern was the great number of pollen types present in bud clusters, buds, and individual anthers in pollen of *C. crassiflora, C. koehneana,* and *C. jorullensis.* These authors felt it was crucial to the interpretation of the pollen data to determine whether the pollen polymorphism suggested heterostyly or if a single basic pollen type with several variations was produced. As discussed by them (Graham et al., 1968: 1087–1088):

> The term "polymorphisme" has been used

to describe the multiple pollen types produced by individual plants or anthers in *Cuphea* (Cos Campos, 1964), but in our opinion use of the term has been preempted by a different situation existing in certain species of *Primula, Lythrum,* and other genera. As early as 1841, Vaucher noted three floral forms in *Lythrum,* and Darwin (1865) made a study of trimorphism in *L. salicaria* L. According to S. Graham (1964), 'In this species there are three style lengths and three sets of stamens of lengths corresponding to those of the styles. The forms are termed long-, mid-, or short-styled, depending on whether the style exceeds, lies between, or is shorter than the two whorls of stamens. Pollen differs in color, size and amount of stored starch in each of the three stamen lengths. The longest stamens have the largest grains, the anthers are green, and the pollen is filled with starch. The two shorter stamen lengths have yellow anthers and correspondingly smaller pollen containing less starch.' Thus *Lythrum salicaria* produces three morphologically distinct kinds of pollen and each is consistently associated with another feature of floral structure, viz., stamen length. In *Cuphea* the multiplicity of pollen types is greater (up to 12 in *C. strigulosa,* fide Cos Campos, 1964, p. 332), occurs within a single anther, and is not correlated with any other feature of the plant.

Therefore, in order to determine the nature of the multiple pollen types in *Cuphea,* size studies of single anther lactic acid preparations were conducted (Graham et al., 1968). The statistical data rather definitively gave support to the idea of normal pollen variations rather than to heterostyly.

A very comprehensive light microscope study by Lee (1979) included 26 genera and 62 species of Lythraceae pollen. Great emphasis was placed on the number of subsidiary colpi and three major pollen groups were established: (1) three-pseudocolpate (*Lythrum, Pemphis, Peplis, Physocalymma, Rhynchocalyx*); (2) six-pseudocolpate (*Ammannia, Capuronia, Crenea, Ginoria, Haitia, Lagerstroemia, Lawsonia, Nesaea, Pleurophora, Rotala*); and (3) non-pseudocolpate (*Adenaria, Alzatea, Cuphea, Decodon, Didiplis, Diplusodon, Galpinia, Grislea, Heimia, Lafoënsia, Rotala*). Based on number of subsidiary colpi this study did not support the tribal classification of Lythraceae (Koehne, 1903) into Lythreae and Nesaeae and their respective subdivisions. All had a mixture of the above three pollen groups. It was also concluded that, based on its non-subsidiary colpate pollen, *Alzatea,* which was originally placed near to *Physocalymma* and *Diplusodon* (Lourteig, 1965), is better assigned near to *Grislea* or *Adenaria.* Also, the placement of *Rhynchocalyx* near *Lawsonia* (Sprague & Metcalfe, 1937) was disputed on the basis of three subsidiary colpi and indistinct pores in the former and six subsidiary colpi and distinct pores in the latter. Both *Alzatea* (Graham, 1984) and *Rhynchocalyx* (Johnson & Briggs, 1984) are now regarded as separate monotypic families.

In the most recent study of Lythraceae, pollen of *Crenea, Diplusodon, Lafoënsia,* and *Lagerstroemia,* as well as *Sonneratia* (subfam. Sonneratioideae), were compared from a harmomegathic functional standpoint, and several structural pollen types were established (Muller, 1981). Starting with a tricolporate, longiax prototype, Muller (1981) postulated that the relationship between pollen form and function was indicative of adaptive radiation in the following directions or series: (1) in the first series there is a trend toward increasing the number of colpi (i.e., subsidiary colpi), (2) in the second series harmomegathic functions are transferred from individual colpi to flexible apertural fields alternating with meridional ridges, (3) in the third series harmomegathic functioning is transferred to prominent pores, and (4) in the last series harmomegathic functioning is lost in the ecto- and endoapertures.

The usefulness of pollen morphology in the taxonomy of Lythraceae is summarized by Muller (1981: 121–122) whereby he emphasizes the need:

> . . . for ecologic interpretations of function and for detailed ultrastructural studies to uncover those characters which reflect ancient phylogenetic links. This can perhaps best be illustrated by a discussion of possible affinities between the genera *Lafoënsia, Lagerstroemia,* and *Sonneratia,* assuming that it is decided to place the latter in the Lythraceae. If convergences in recent pollen morphology are stressed, *Lafoënsia* would be considered closely related, but the differences in ultrastructure and the heterocolpate nature in some pollen types of this genus would argue against affinity with *Sonneratia.* If fossil evidence is taken into account, the genus *Lagerstroemia* appears a much

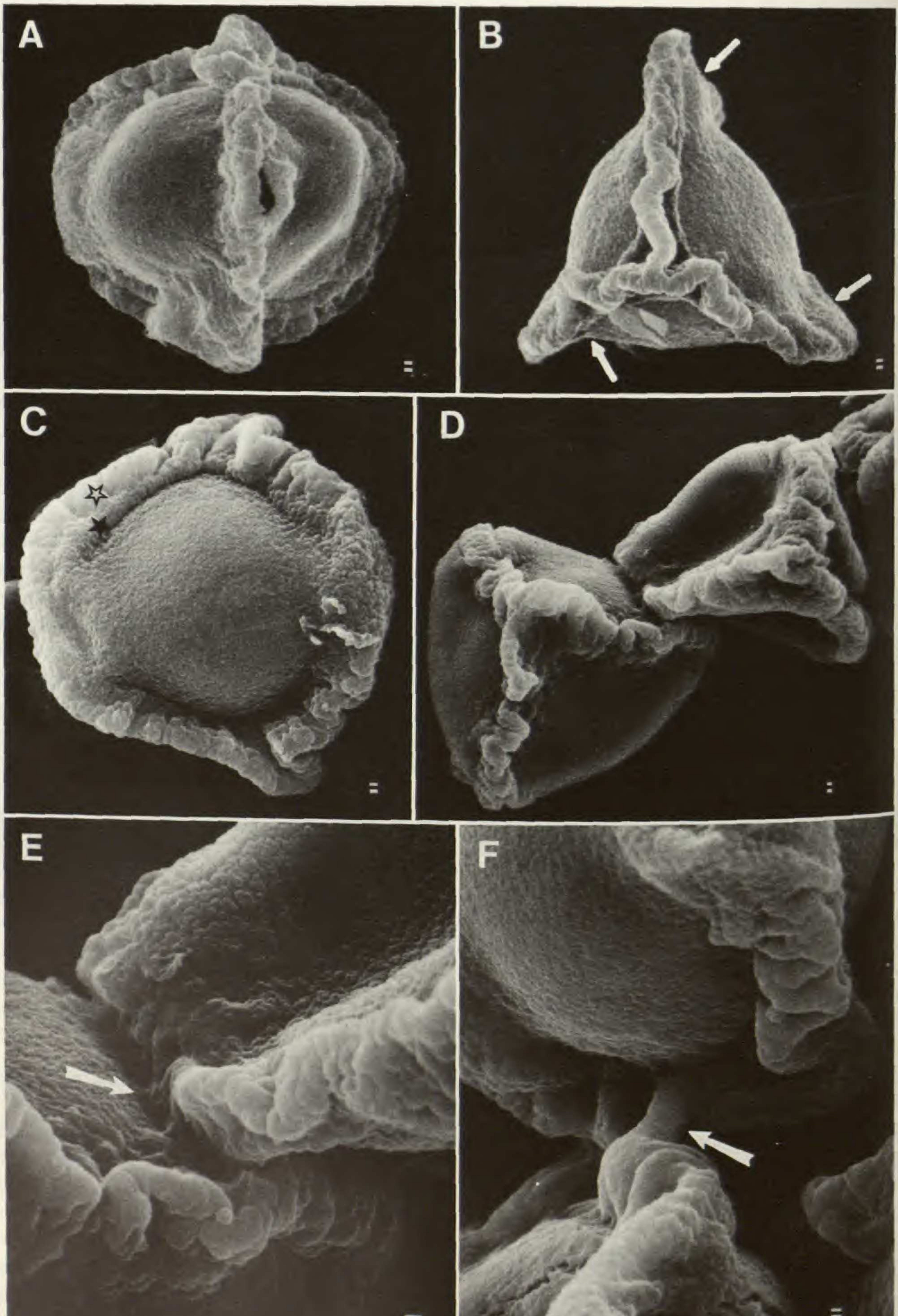

FIGURE 9. Scanning electron micrographs of Trapaceae pollen. A–F. *Trapa natans.*—A. (*Engelmann s.n.*). Lateral view showing three meridional ridges. The vertically cracked area of the dome in the central ridge exposes part of the colpus.—B. (*Engelmann s.n.*). Polar view. The three protruding domes (arrows) are covered by meridional ridges, which in turn, are united at the pole.—C. (*House 21708*). Lateral view of the area between two meridional ridges. Note that the ridges are continuous over the domed areas. The two-part nature of the

stronger candidate, although its present-day types show less similarity with living *Sonneratia* types, having diverged rather strongly from a postulated common ancestral matrix, although the peculiar granular deposits in the intercolumellar space appear to be present both in *Lagerstroemia* and *Sonneratia.*

In a more general sense and concerning the taxa examined in this study (Table 1), *Lafoënsia* is similar to *Sonneratia* of subfam. Sonneratioideae (Muller, 1969, 1978a, 1981, Fig. 4E); *Diplusodon* is similar to *Duabanga* of subfam. Duabangoideae (Muller, 1981; Fig. 4F); and *Lagerstroemia* bears resemblance to *Punica* (subfam. Punicoideae, Fig. 7D, F). These similarities strongly support the view of Dahlgren and Thorne (1984) that *Sonneratia, Duabanga,* and *Punica* should be regarded as separate subfamilies independently related to Lythraceae.

TRAPACEAE

Trapa japonica and *T. natans* were examined with SEM and TEM. Pollen from both species are basically similar. They are tricolpate, radially symmetrical, isopolar, spheroidal in lateral view; and triangular, goniotreme with obtuse corners, and straight to convex sides in the polar view (Figs. 9, 10). There are three meridional ridges on the grains. The surface is granular. The three apertures are protruding and swollen as elongated domes. In *T. japonica* these domes are better developed than in *T. natans.* Within them there is an elongated lens-shaped opening or colpus (Erdtman, 1943: 104–105, figs. 221–223) which is not visible in scanning electron micrographs as it is covered by the meridional ridge. The meridional ridges are formed by the folding of the ektexine and they are united at both poles where their fused triangular base is greatly enlarged (Figs. 9B, 10B). The ridges are taller at the poles; as they extend toward the equator in a folded, undulating manner their height decreases. The surface at the upper portion of the ridge near the poles is smooth with many channels. The lower portion shows a granular-verrucate surface (Fig. 9C). Toward the equator, the upper portion of the ridge is more rugulate-verrucate. Over the colpi, the upper portion of the ridge continues as a wide and not very tall, verrucate-granular band. The lower portion spreads over the swollen domes and is continuous with the surrounding interapertural areas (Fig. 10C–E). The surface of the domes is granular like that on the mesocolpia. It is not clear how the colpi open, but they appear to do so by an irregular splitting of the exine (Figs. 9A, 10D, F).

One sample of *Trapa natans* (*House 21708*) showed clumps of grains (polyads?) along with free monad grains. Exinous connections between the members of these "polyads" are present (Fig. 9D–F). However, there is no discernible specific arrangement of the polyad members, and the bridges connect different parts of the adjacent grains. This phenomenon is not yet clearly understood.

In *T. natans* the fine, granular surface of the grain is due to the tightly packed clavate and rod-shaped elements that form a very thin layer as seen in the thin sections (Fig. 11A–C). These clavae are either solid in their entire length, or show a fine, fuzzy granular layer below them. The exine structure of *T. japonica* (Fig. 11D) is similar to *T. natans* but the fuzzy layer is not evident. When cut obliquely, the clavate layer appears to be beaded and spongy. The thick, more or less solid layer below the fuzzy layer appears to be the endexine which becomes granular near the pores. The foot layer is difficult to recognize but it is perhaps present as a very thin layer between the fuzzy layer and the solid endexine. On the granular endexine near the pores, such a layer is clearly visible.

Sections passing through the ridge show that it encloses a cavity (star in Fig. 11A). The clavate layer (CL in Fig. 11A), along with the fuzzy granular layer (G in Fig. 11A), lifts to form the ridge wall. It continues as such for a short distance (i.e., the granular lower portion of the ridge as seen from the outside and designated by a solid

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ridge is indicated by the stars: the open star shows the upper part which is highly folded, the solid star shows the lower part which is granular.—D. One sample of *T. natans* (*House 21708*) contained numerous fused grains (polyads). A part of such a polyad is shown here.—E. (*House 21708*). Enlarged area of Figure 7D showing fusion of two adjacent exine surfaces.—F. (*House 21708*). Extexinous bridges appear to be another mechanism of pollen grain adhesion: the arrow shows a bridge connecting the meridional ridges of two pollen grains. Scales equal 1 μm.

star in Fig. 9C) and then becomes a more or less discontinuous, solid layer (the psilate upper portion of the ridge seen from the outside, the open star in Fig. 9C). The inner margin of this solid layer is highly irregular. Clavae at the base of the ridge cavity are large and often appear to be branched. Just above these clavae, the cavity is filled with circular or elongate ektexinous elements.

Discussion

Structurally, the meridional ridge of *Trapa* is different from that found elsewhere in the order. It is formed by the uplifting and folding of the ektexine and encloses a cavity. In contrast, the ridge found in Lythraceae (*Lagerstroemia,* see also van Campo, 1966; and *Punica*) and Onagraceae (*Ludwigia*) is formed by the increased thickness of the exine. Moreover, the ridge passes over the colpi in *Trapa,* whereas it alternates with the colpi in the other groups.

The distinctiveness of *Trapa* pollen was recognized by Erdtman (1971), who examined three species and felt that the genus merited family status. *Trapa* pollen shows a distant resemblance to Onagraceae pollen in surface sculpture and in the nature of the protruding apertures (see Figs. 50–53 of Onagraceae pollen below). Similarities to Onagraceae are further evident in the very thick endexine and indistinguishable, or at least, very thin, foot layer (compare Figs. 11 and 60–63).

OLINIACEAE

Olinia emarginata, O. radiata, O. rochetiana, O. vanguerioides, and *O. ventosa,* which comprise all species of the family, were examined with SEM and TEM. Pollen from all of the species is remarkably similar, both at the exomorphological and the endomorphological levels.

Pollen is tricolporate, radially symmetrical, ovoidal to subovoidal in lateral view (Muller, 1978b) and circular to triangular in polar view (Figs. 12, 13). It is heteropolar because the plane

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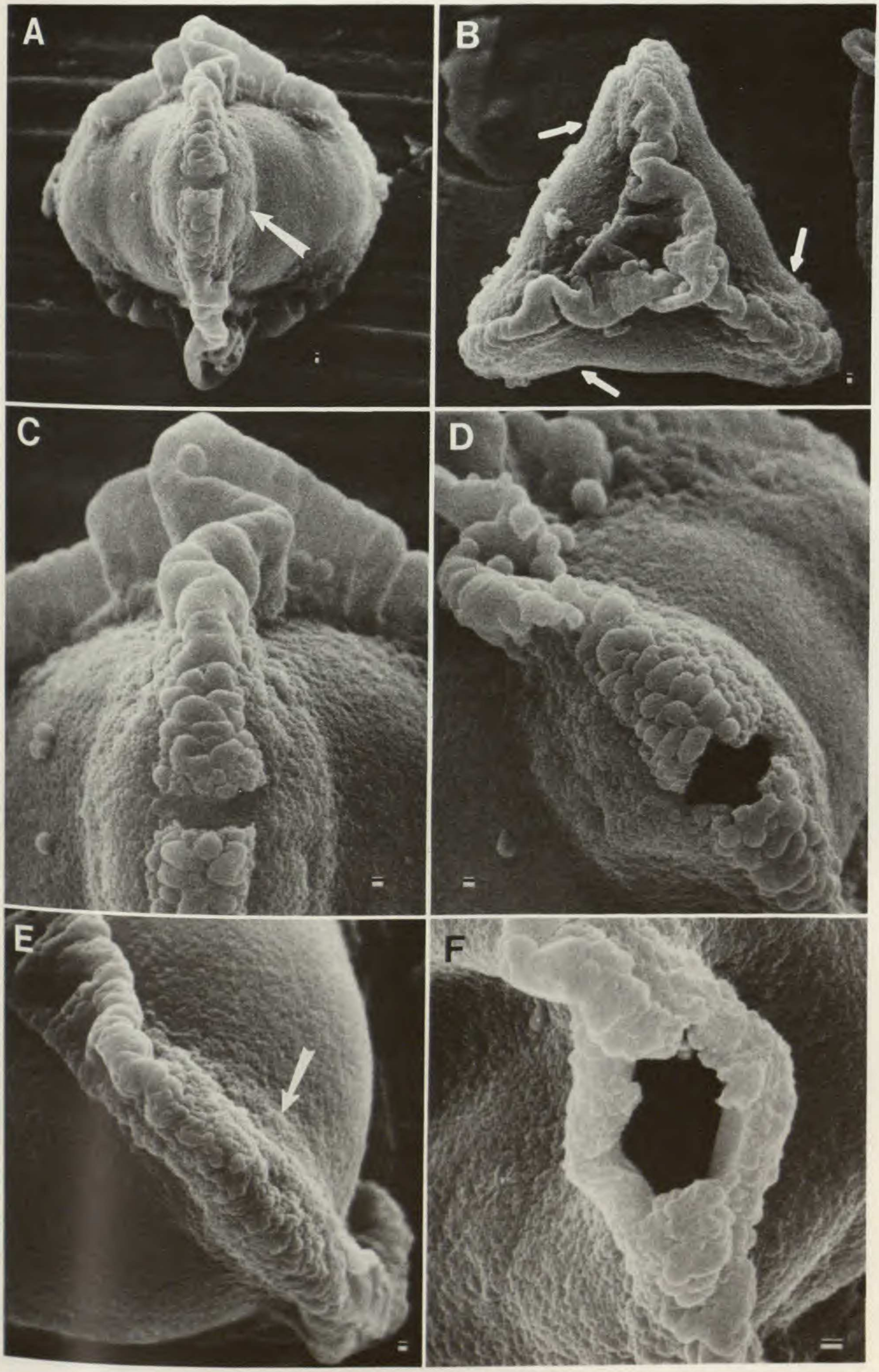
FIGURE 10. Scanning electron micrographs of Trapaceae pollen. A–D. *Trapa japonica.*—A. Lateral view with a domed area (arrow) and a meridional ridge that passes over it (in this grain the ridge is discontinuous at the equator). The maximum height of the ridge is at the poles. An elongated lens-shaped colpus is enclosed within this domed area which is only visible with light microscopy (Erdtman, 1943, Pl. XIII, figs. 221–223).—B. Polar view showing three protruding, domed areas (arrows) and the three ridges that unite at the poles.—C. Surface detail of A.—D. Close-up of domed area which has split horizontally. E, F. *Trapa natans.*—E. (MO 2532983). Close-up of domed area (arrow) which is less prominent than in *T. japonica* (see A, C, D). The ridge is composed of verrucate, granular elements.—F. (*Engelmann s.n.*). View showing irregular splitting of the ridge in the dome area. Scales equal 1 μm.

FIGURE 11. Transmission electron micrographs of Trapaceae pollen. A–C. *Trapa natans.*—A. (*Engelmann s.n.*). Section of the meridional ridge with cavity (star) and surrounding area. The upper portion of the ridge (within bracket) is essentially homogeneous; the lower portion has a clavate layer (CL) over an expanded granular layer (G). Large, solid, irregular elements (unlabeled arrow) are present at the base of the ridge cavity. The endexine (en) is extremely thick and uniform.—B. (*House 21708*). Section of colpus. The endexine is thick, granular (star), and finely lamellate. The absence of endexine (bracket) indicates a colpus which is a lens-shaped meridional area (not evident here, see Fig. 10A legend discussion). This area is covered by clavae and a coarsely granular layer (arrow).—C. (*House 21708*). Two sections of the mesocolpium. The ektexine is thin and composed of tightly packed clavae with a fuzzy basal layer (arrowhead). The foot layer cannot be readily distinguished and the endexine is thick (significantly thicker than the ektexine).—D. *Trapa japonica.* Section of a mesocolpium. In all transmission electron micrograph preparations of *Trapa* pollen, the endexine has shown little, if any, difference in electron density from the ektexine. Studies with fresh pollen should help to clarify this exine layer, as well as the presence or absence of the foot layer. Scales equal 1 μm.

FIGURE 12. Scanning electron micrographs of Oliniaceae pollen. A–C. *Olinia radiata.*—A. Polar view showing the polar face without subsidiary colpi.—B. Lateral view. The colpus is asymmetrical with the long segment extending into the polar face that lacks subsidiary colpi (lower half in this figure) and the short segment extending into the polar face that has the subsidiary colpi (a subsidiary colpus is indicated between arrows). An elliptic, lalongate endoaperture is discernible at the modal plane.—C. Polar view showing the polar face that has three subsidiary colpi alternating with the short segments of the colpi. D–F. *Olinia rochetiana* (*Chapman 996*).—D. Subpolar view. Arrow points to a partially visible subsidiary colpus.—E. Polar view. Subsidiary colpi with a rugulate-granular surface alternate with short segments of the colpi.—F. Polar view of the polar face that does not have subsidiary colpi. Scales equal 1 μm.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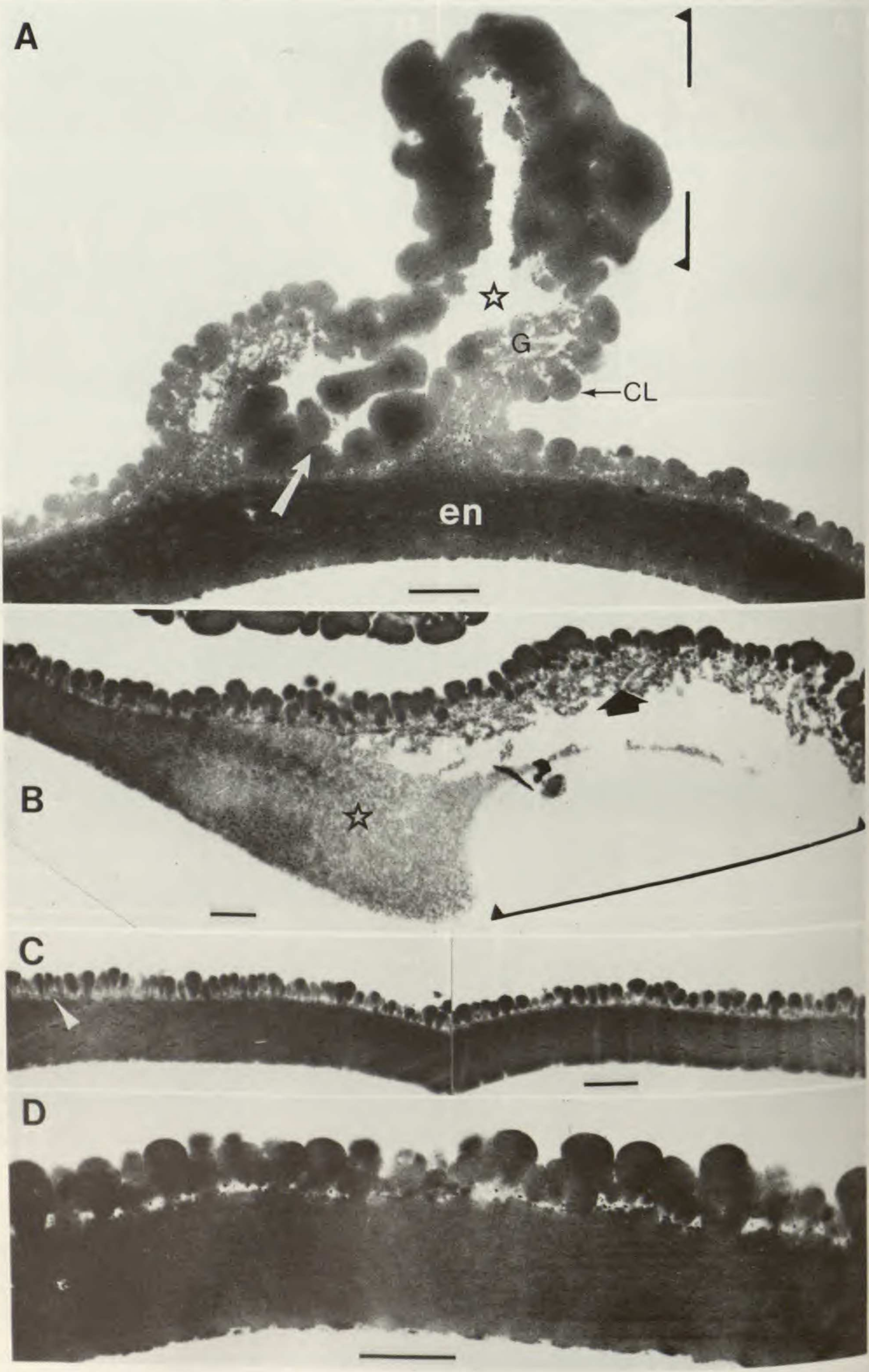
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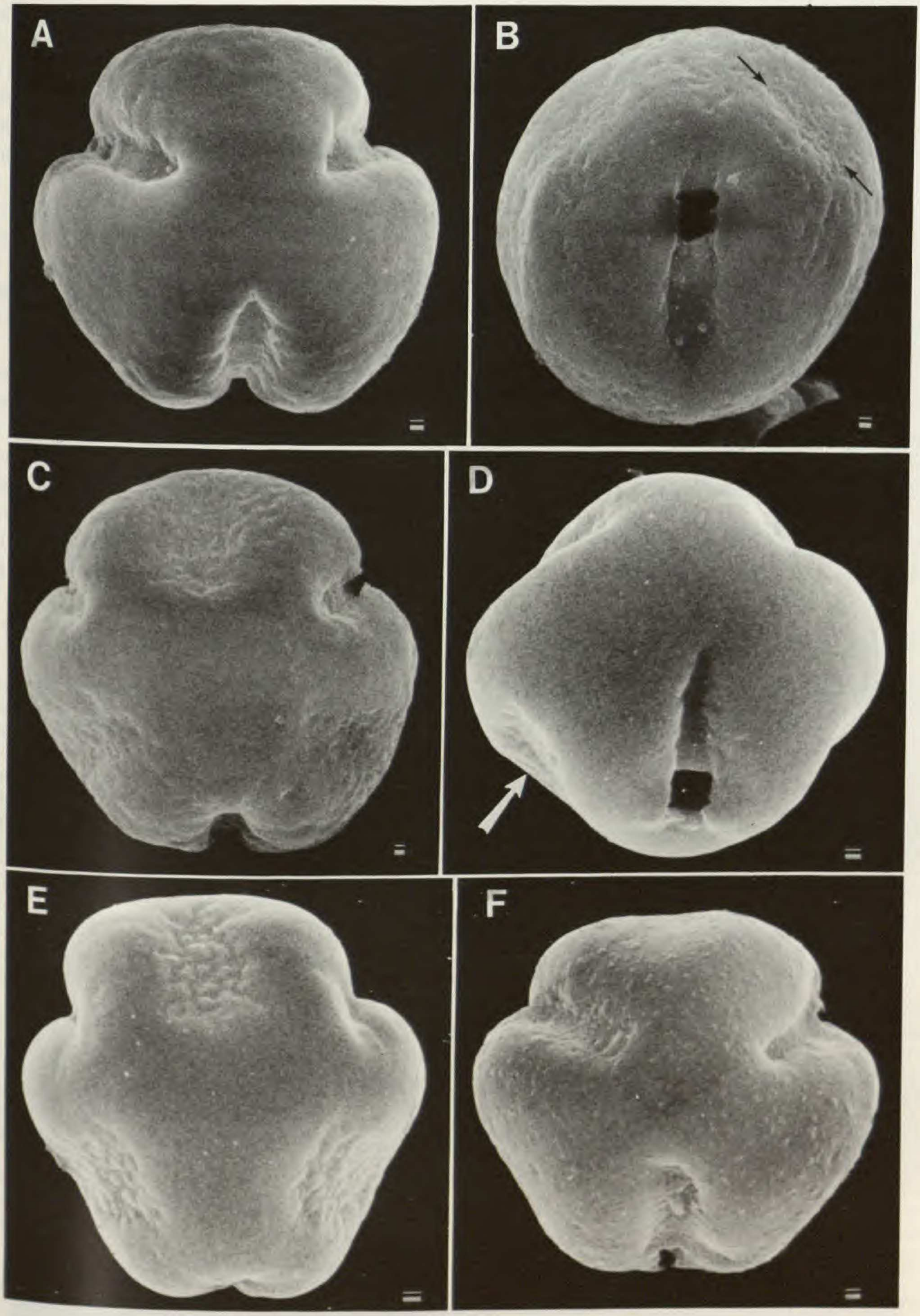
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that is perpendicular to the polar axis and situated at the greatest width of the grain divides it into two unequal polar faces. This is referred to as the modal plane (Muller, 1978b). The surface is usually psilate, or rarely psilate-punctate as in *O. radiata* (Fig. 12B, C).

The aperture system in *Olinia* is unusual in that the pollen grains have asymmetrical colpi and half subsidiary colpi (Patel et al., 1983b). Each colpus consists of a long segment and a short segment. The long segments are on the larger polar face of the grain (Fig. 12A, F) and they are slightly wider than the short segments (Fig. 13A, F). The surface of the colpi is smooth or granular and the ends are acute. An elliptic, lalongate endoaperture is present on the modal plane where the two segments of the colpus meet. The endoapertures are covered by extensions of the mesocolpia.

The second unusual character of *Olinia* pollen is the presence of three half subsidiary colpi which do not extend into both polar faces of the grain. They are present on the polar face that has the short segments of the colpi. Their surface is rugulate, with irregular, branched channels (Figs. 12C–E, 13A, D–F). They are often wide and therefore tend to resemble intercolpar concavities. This type of aperture system can also account for the grains being heteropolar. However, in some grains a size difference between the two polar faces is not evident and such grains are spheroidal in lateral view. Rarely, the subsidiary colpi extend slightly beyond the equator into the opposite polar face.

The ektexine in the mesocolpia consists of a very thick foot layer (Fig. 14) which becomes extremely thick toward the colpi (Fig. 14D, E). From the foot layer arise the thick and short, often prostrate or irregular-mound-like columellae which are usually narrower at their distal ends where they form an infratectal granular layer (Fig. 14C). The tectum is thick, uniform and

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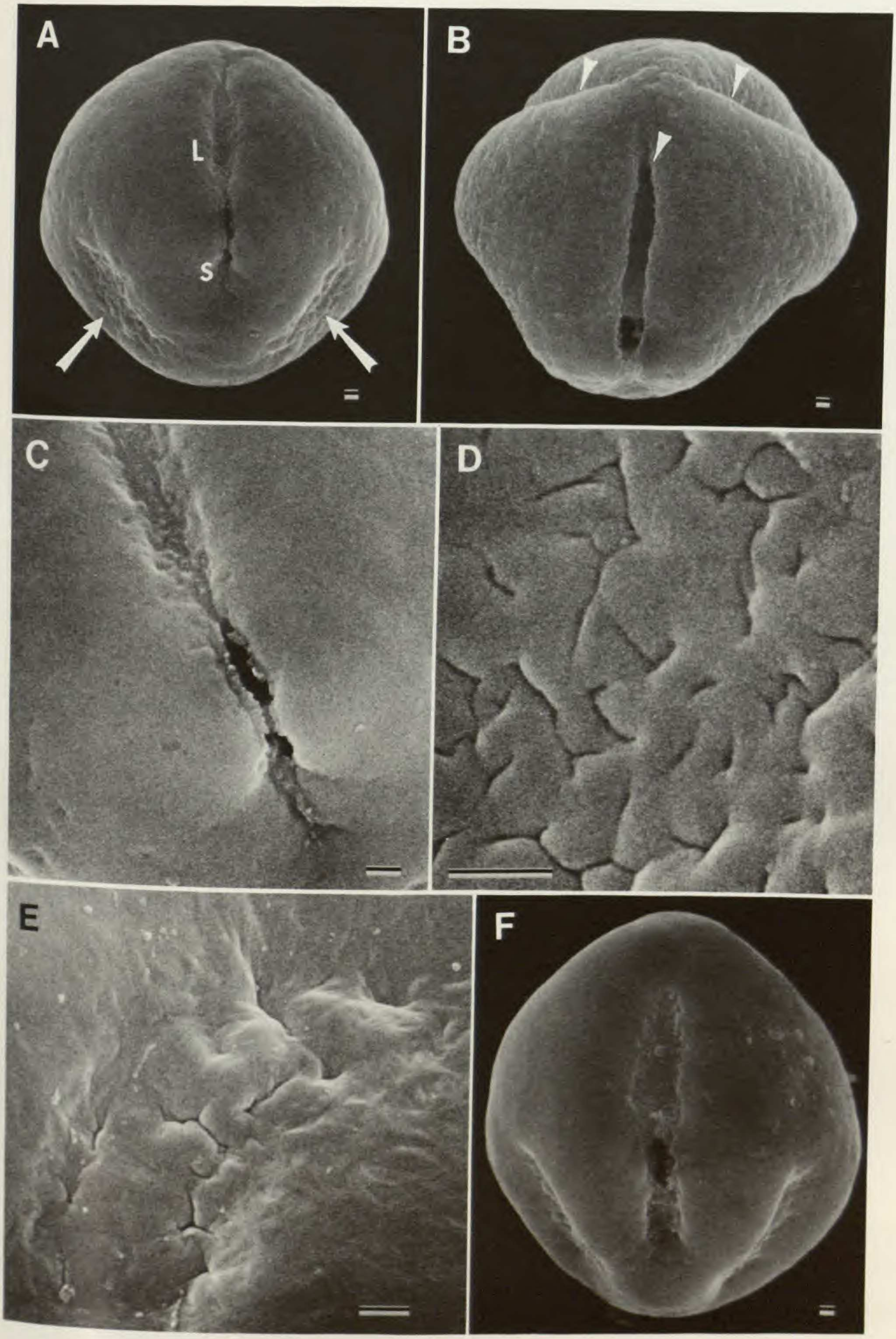
FIGURE 13. Scanning electron micrographs of Oliniaceae pollen. A–D. *Olinia emarginata.*—A. Lateral view clearly showing two subsidiary colpi (arrows) alternating with the short segment (S) of the colpus on the lower polar face. The upper polar face has the long segment (L) of the colpus and no subsidiary colpi.—B. Subpolar view showing the polar face that lacks subsidiary colpi. The long segments of the three colpi are visible (arrowheads).—C. Details of part of the colpus of A.—D. Details of a subsidiary colpus showing a rugulate smooth exine surface with irregularly branched channels. E, F. *Olinia ventosa.*—E. View of a subsidiary colpus with a rugulate surface.—F. Lateral view showing two subsidiary colpi, asymmetrical colpus, and psilate exine surface. Scales equal 1 μm.

FIGURE 14. Transmission electron micrographs of Oliniaceae pollen.—A. *Olinia rochetiana* (*Chapman 996*). Section of a subsidiary colpus. The rugulate surface elements described in scanning electron micrograph (Fig. 12E) appear in transmission electron micrograph as a dome-shaped tectum below which is an infratectal granular layer. Columellae are absent and the foot layer (arrowhead) is narrow but consistent over the subsidiary colpus. The endexine (en) is thick and uniform. B, C. *Olinia ventosa.*—B. Section of a mesocolpium. The tectum is uniform, thick, and imperforate. The arrow indicates an infratectal granular layer immediately beneath the tectum. Columellae are extremely short. The foot layer is nearly as thick as the tectum and the underlying endexine is uniform and approximately one-half the thickness of the foot layer.—C. Section includes a mesocolpium (right of bracket) and part of subsidiary colpus (left of bracket). Note the prominent thickening of the endexine under the subsidiary colpus.—D. *Olinia rochetiana* (*Greenway & Fitzgerald 14970*). Section through the aperture region including part of the endoaperture (at the left). The mesocolpial extension over the endoaperture is indicated by the bracket. The thick tectum is gently undulating and imperforate; the infratectal granular layer is prominent and is supported by short but stout columellae. The foot layer (fl) is thickened at the endoaperture margin; similarly, the endexine also is thickened as well as being markedly granular.—E. *Olinia emarginata.* Section passing through endoaperture. The arrow within the endoaperture indicates free "hanging columellae" and disrupted foot layer typical of this area. Note underlying granular endexine. The sections in Figure 14 resemble the sections of Penaeaceae pollen in Figures 26 and 27. Scales equal 1 μm.

FIGURE 15. Scanning electron micrographs of Combretaceae pollen. A–C. *Combretum cacoucia.*—A. Polar view showing three colpi with extensions of mesocolpia over the endoapertures and three subsidiary colpi.—B. Lateral view. The endoaperture appears as a wide elliptic shadow. The colpus membrane is granular. Two subsidiary colpi are also visible.—C. Finely regulate surface in polar view. D, E. *Thiola inundata.*—D. The exine surface consists of echinate plate-like areas that are delimited by channels and punctae. The colpus has echinae over the endoaperture (arrow).—E. Subpolar view showing three apertures and three subsidiary colpi.—F. *Quisqualis indica.* Polar view. The three subsidiary colpi are wide and appear to be more like intercolpar concavities.—G. *Calycopteris floribunda.* Sublateral view showing a subsidiary colpus (center) alternating with colpi. The exine surface is rugulate. Scales equal 1 μm.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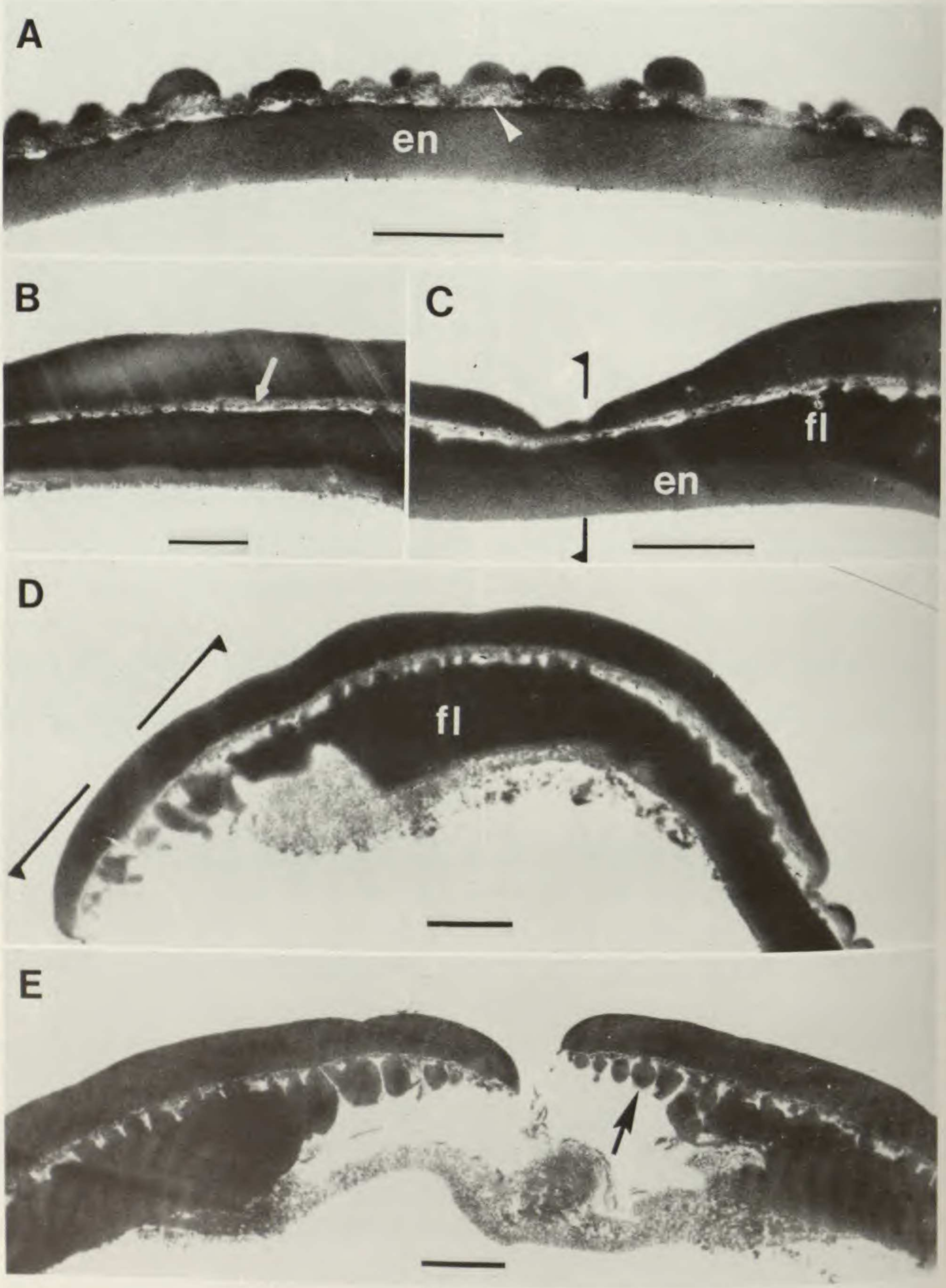
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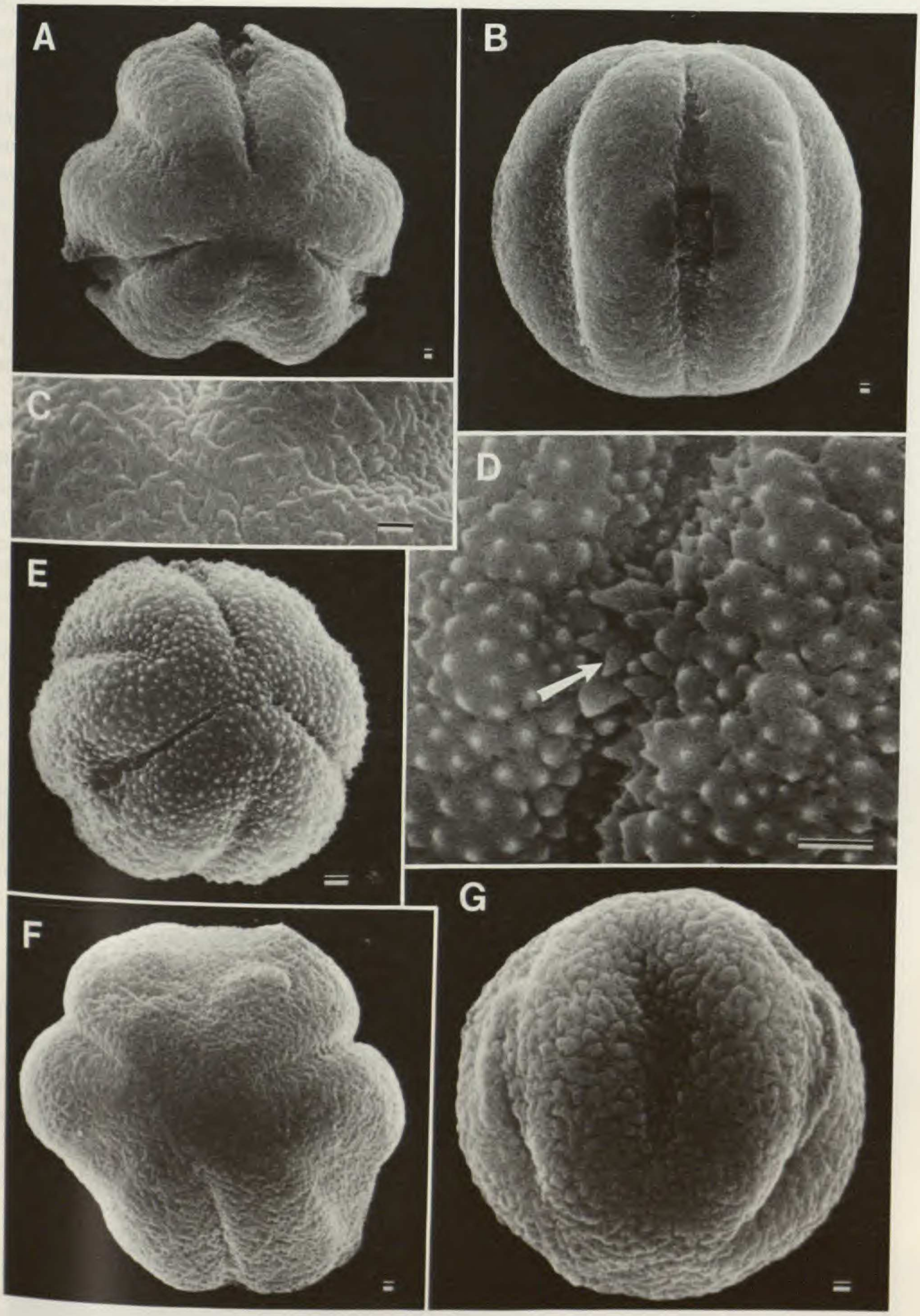
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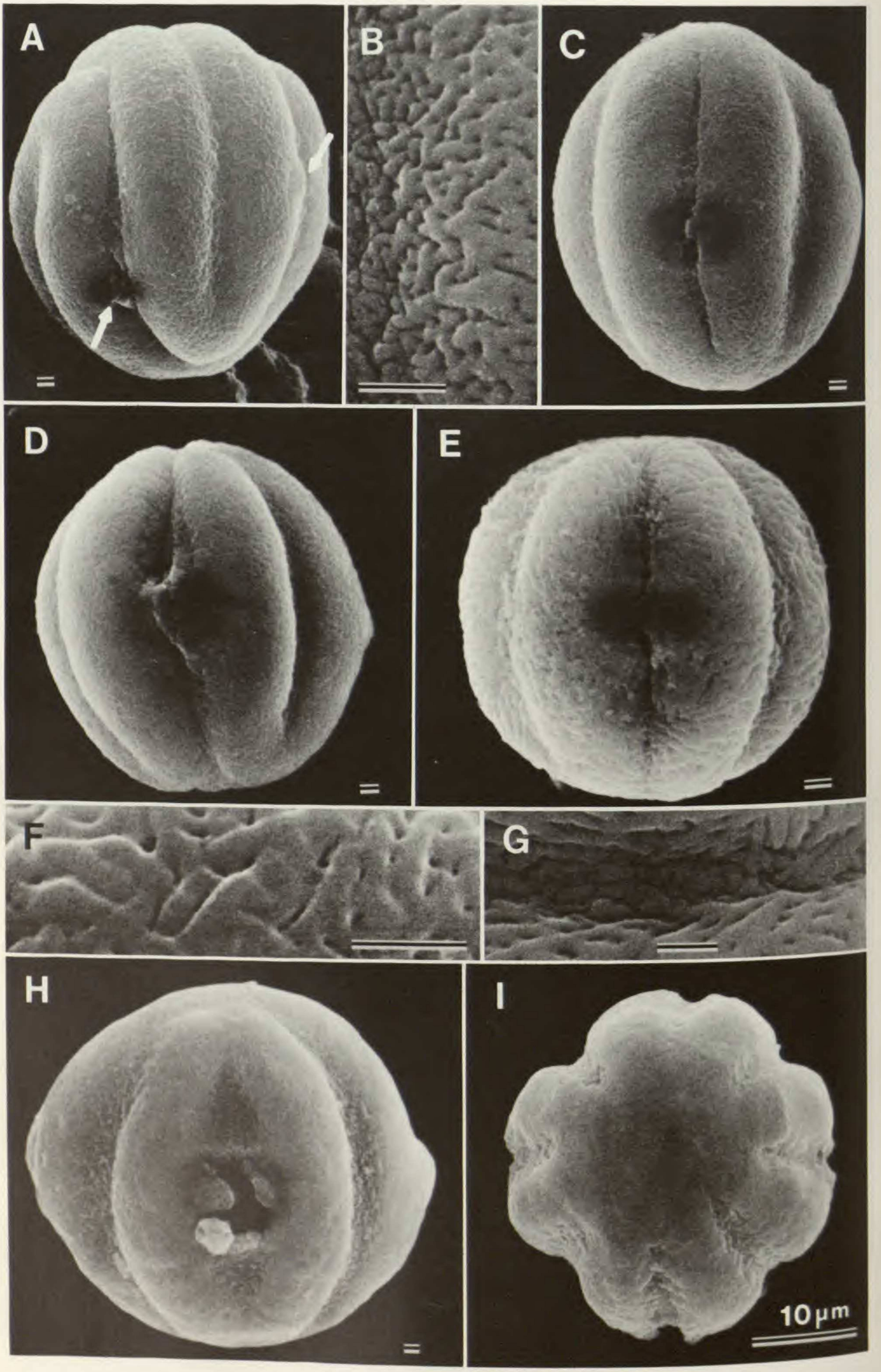
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without perforations (except in *O. radiata*). The upper margin of the tectum is smooth. The endexine is thin but becomes markedly thickened in the colpi and subsidiary colpi regions. The subsidiary colpi show a thinner, undulating, often dome-shaped tectum (Fig. 14A). The infratectal granular layer is continuous here. The columellae appear as short connections between it and the very thin, discontinuous foot layer.

In the area of the endoapertures (Fig. 14D, E), the endexine is granular. The extensions of the mesocolpia show a disrupted thin foot layer, and a thin infractectal granular layer below a slightly thinner tectum.

Discussion

Oliniaceae pollen grains differ from all other groups in their unusual aperture system, i.e., the asymmetrical colpi and the half subsidiary colpi (Patel et al., 1983b). All species examined are very similar in exo- and endomorphology and are difficult or impossible to distinguish. Erdtman (1971) reported three subsidiary colpi in *O. cymosa* (= *O. ventosa*) and that subsidiary colpi were absent in *O. volkensii* (= *O. rochetiana*). Samples of *O. rochetiana* examined in this study show half subsidiary colpi and asymmetric colpi, similar to the other species of *Olinia*. Since half subsidiary colpi occupy small areas on only one polar face and differ only slightly in surface sculpturing from the surrounding exine, it is not surprising that their true nature is difficult to reveal with the light microscope. However, in the light micrograph of *O. rochetiana* by Archangelsky (1971, fig. 1, Pl. 20), three half subsidiary colpi are clearly visible.

Apart from the unusual apertures, the colpi and the half subsidiary colpi, pollen of Oliniaceae resembles that of Penaeaceae. Pollen from both families compare very well in the psilate surface as well as in exine structure, that is, there is a very thick foot layer and tectum, and a thin columellae layer with an infratectal granular layer extending over the subsidiary colpi (compare Fig. 14 to Fig. 26).

COMBRETACEAE

Pollen is tricolporate (rarely tetracolporate in *Quisqualis parviflora* and *Terminalia oblonga*), mostly heterocolpate (except in *Buchenavia, Laguncularia,* and *Strephonema*), radially symmetrical, and isopolar. The shape of the grains is spheroidal to subprolate in lateral view and circular to hexagonal in polar view. In the heterocolpate species, the colpi are long, with acute ends, and with a granular surface. Syncolpate grains are present in *Combretum farinosum* (Fig. 16D) and in *T. oblonga* (Fig. 16A) where the syncolpus is undulating like the line on a tennis ball. Endoapertures are lalongate and elliptic in *Combretum cacoucia* (Fig. 15B), *C. laxum* (Fig. 16E), and *Lumnitzera racemosa* (Fig. 19D), circular in *Poivrea coccinea* (Fig. 19C) and *Anogeissus acuminata* (Fig. 18D), and circular to elliptic in *Bucida macrostachya* (Fig. 17A), *C. farinosum* (Fig. 16D), *Q. parviflora* (Fig. 16H), and *T. oblonga* (Fig. 16A, C). Subsidiary colpi are wide and often united at the poles in *Ramatuella argentea* (Fig. 17E), *Terminalia catappa, T. oblonga* (Fig. 16A), and *Guiera senegalensis* (Fig. 18E).

Diverse surface sculpture patterns are present in the family. The surface is striate in *Combretum laxum, Guiera,* and *Poivrea.* In *C. laxum* (Fig. 16E, G), thick striae are separated by short, punctate channels while the surface of the subsidiary colpi is striate-rugulate. In *Guiera* (Fig. 18E), small groups of short striae cross, and the subsidiary colpi appear to have a finer, granular, striate surface. *Poivrea* (Fig. 19C) shows bands of fine, long striae while the subsidiary colpi are striate-rugulate.

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FIGURE 16. Scanning electron micrographs of Combretaceae pollen. A–C. *Terminalia oblonga.*—A. Lateral view of a tetracolporate, syncolpate grain. The subsidiary colpi are also united. Note that the two visible endoapertures (arrows) are situated at two different horizontal planes of the grain.—B. Finely rugulate surface of a mesocolpium (right half) near a subsidiary colpus (left half). The rugulate-punctate surface becomes finer in the subsidiary colpus.—C. Lateral view of a tricolporate grain.—D. *Combretum farinosum.* Lateral view of a tricolporate, syncolpate grain. E, G. *Combretum laxum.*—E. Lateral view. Note the striate-rugulate surface.—G. Striate-rugulate surface of a subsidiary colpus and striate surface of the two surrounding mesocolpia.—F. *Combretum trifolium.* Surface of a mesocolpium showing interwoven muri and punctae. Compare with Figure 15C. H, I. *Quisqualis parviflora.*—H. Lateral view of a tricolporate grain.—I. Polar view of a tetracolporate grain. Compare with Figure 23B. Unless otherwise indicated, scales equal 1 μm.

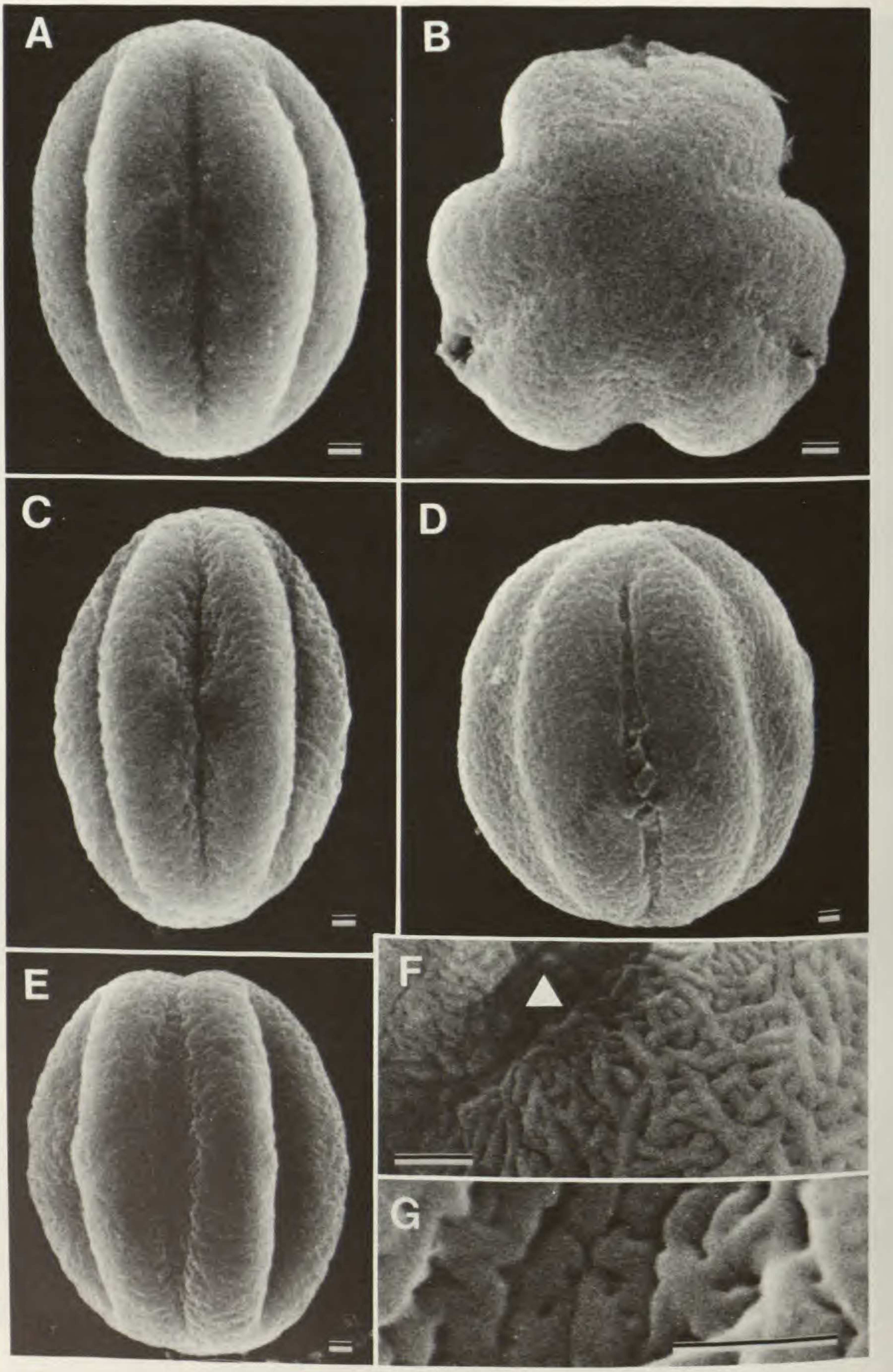

FIGURE 17. Scanning electron micrographs of Combretaceae pollen.—A. *Bucida macrostachya.* Lateral view showing a colpus (at center) and two subsidiary colpi.—B. *Conocarpus erecta.* Polar view with mesocolpial extensions over the apertures. Also note three subsidiary colpi.—C. *Pteleopsis myrtifolia.* Lateral view with a colpus (at center) and two subsidiary colpi.—D. *Terminalia edulis* (*Quisumbing Q-2156*). Lateral view with a colpus (at center) and two subsidiary colpi. E, G. *Ramatuella argentea.*—E. Lateral view with a subsidiary colpus (at center) and two colpi.—G. Surface detail of a rugulate subsidiary colpus.—F. *Terminalia catappa.* Surface of the mesocolpium near colpus and endoaperture (triangle). Elongate, branched, interwoven elements form the surface sculpture. Scales equal 1 μm.

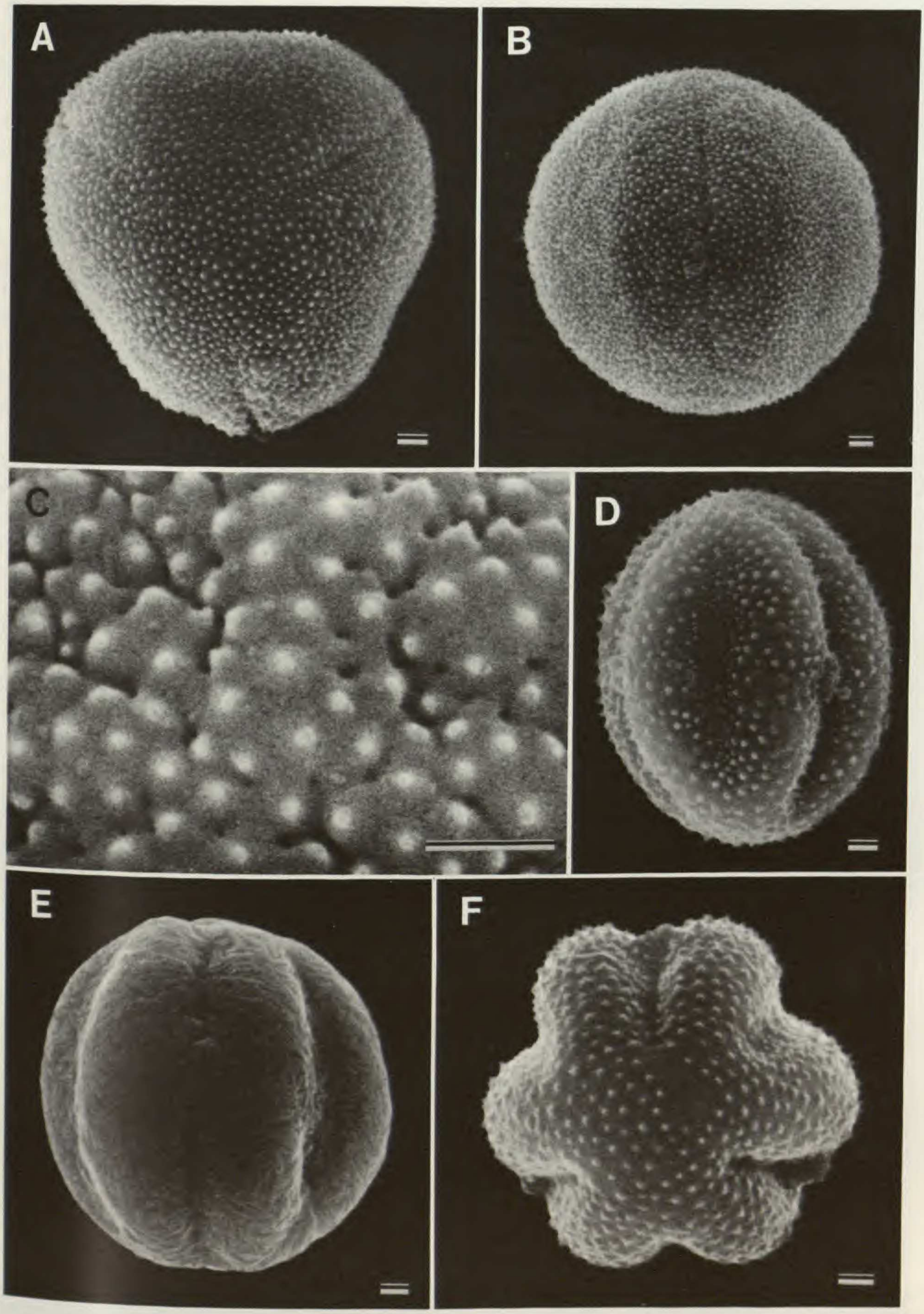

FIGURE 18. Scanning electron micrographs of Combretaceae pollen. A–C. *Buchenavia suaveolens.*—A. Polar view. Colpi are narrow (subsidiary colpi are absent) and the surface is echinate.—B. Lateral view.—C. Details of the echinate-punctate surface. Note similar surface in *T. inundata* (Fig. 15E). D, F. *Anogeissus acuminata.*—D. Lateral view with a wide and granular subsidiary colpus (at center). Two colpi are also evident. The exine surface is echinate.—F. Polar view showing colpi alternating with subsidiary colpi.—E. *Guiera senegalensis.* Lateral view with a colpus at center and two subsidiary colpi. The exine surface is striate. Scales equal 1 μm.

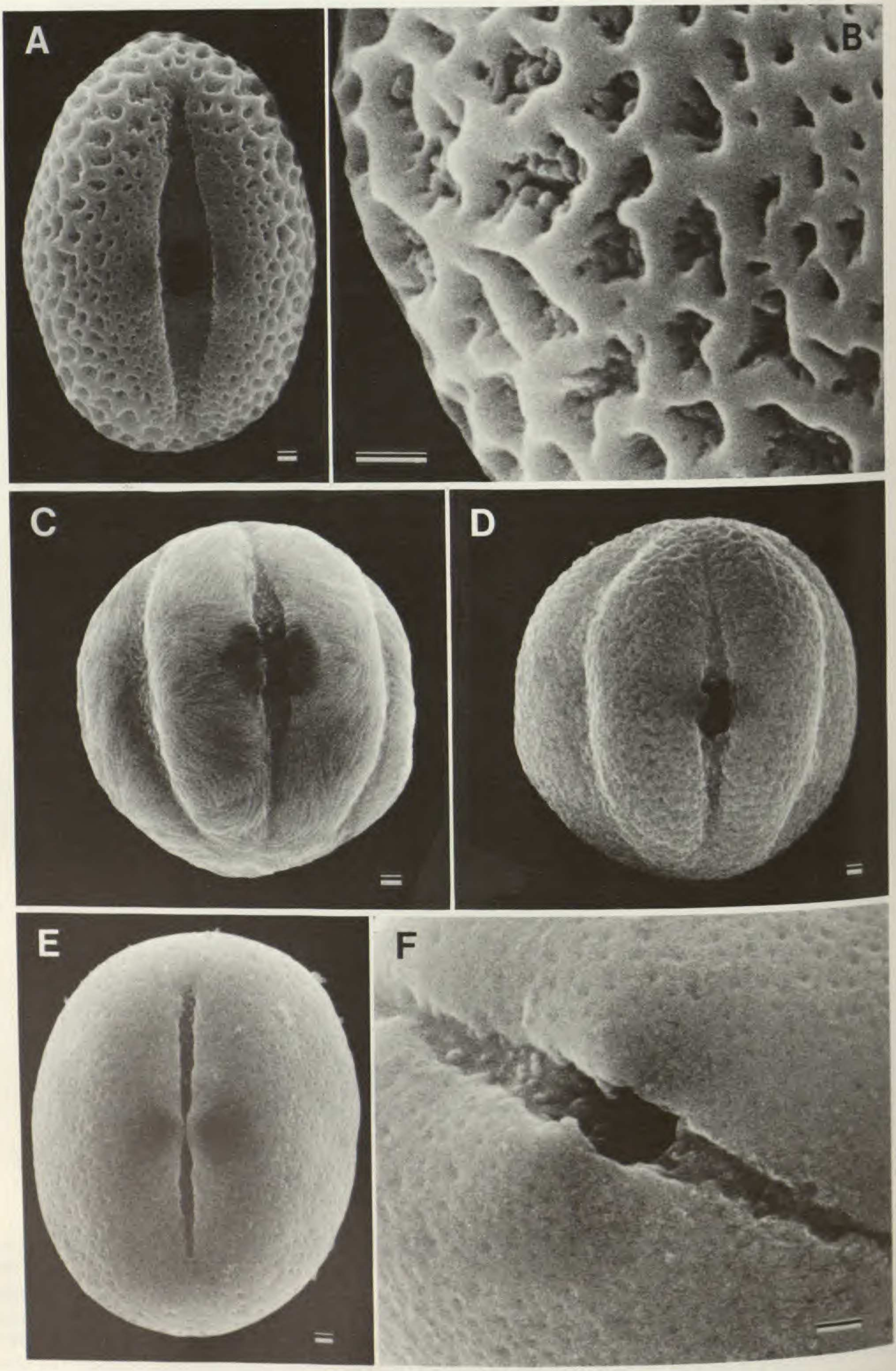

FIGURE 19. Scanning electron micrographs of Combretaceae pollen. A, B. *Strephonema pseudocola*.—A. Lateral view. The exine surface is reticulate with lumina becoming smaller toward the colpus. The partially opened endoaperture is lalongate-elliptic.—B. Detail of the surface showing rod-shaped elements in the larg

In *Combretum trifolium* (Fig. 16F), *Quisqualis indica* (Fig. 15F), *Ramatuella* (Fig. 17E, G), *Terminalia edulis* (Fig. 17D), and *T. catappa* (Fig. 17F) narrow, elongated, and branched muri appear tightly interwoven. Punctae are present in the channels separating the muri. The pattern is finer at the margins of the mesocolpia and less so at the poles where it appears to be punctate in *Q. indica.* The surface of the subsidiary colpi is rugulate-granular in *Ramatuella* (Fig. 17G), and *C. trifolium.* In *Q. indica* (Fig. 15F), the subsidiary colpi are wider than in the other taxa examined and their surface appears to be similar to the surface on the meso- and apocolpia. In *Q. parviflora* the surface is psilate (Fig. 16H, I).

In *Combretum farinosum, Bucida* (Fig. 17A), *Pteleopsis myrtifolia* (Fig. 17C), and *Conocarpus erecta* (Fig. 17B), the surface is more or less smooth to finely rugulate with punctae and short channels that are more pronounced at the margins of mesocolpia. In *Combretum cacoucia* (Fig. 15A–C) and *Terminalia oblonga* (Fig. 16A–C) the surface is finely rugulate. The subsidiary colpi in *C. farinosum, C. cacoucia, Bucida, T. oblonga,* and *Conocarpus* show a coarse, granular-verrucate surface.

A rugulate surface is present in *Lumnitzera racemosa* (Fig. 19D) and *Calycopteris floribunda* (Fig. 15G). In *Lumnitzera* the surface of the subsidiary colpi appears to be granular, whereas in *Calycopteris* it is rugulate-verrucate with slightly smaller rugulate elements than on the mesocolpia.

Anogeissus acuminata (Fig. 18D, F) and *Thiola inundata* (Fig. 15D, E) have an echinate surface with spinules. In *Anogeissus,* scattered spinules are situated on a smooth surface. They become smaller and more numerous at the margins of the mesocolpia. They are also present on the subsidiary colpus and the colpus membrane over the endoaperture. In *Thiola,* in addition to the spinules, there are large punctae and deep channels that also have punctae. Due to the channels, the surface appears to consist of more or less fused "plates or islands" (Fig. 15D). The surface of the subsidiary colpi also has spinules and punctae. Longer spinules are present on the colpus membrane over the endoapertures.

Buchenavia suaveolens, Laguncularia racemosa, and *Strephonema pseudocola* are without subsidiary colpi. In *Buchenavia* (Fig. 18A–C), grains are spheroidal in lateral view and triangular in polar view. The surface is echinate, like that in *Thiola,* with spinules, punctae, and deep channels forming "plates." Colpi are long and narrow. Endoapertures are lalongate. In *Laguncularia* (Fig. 19E, F), grains are subprolate in lateral view and circular to triangular in polar view. The surface is smooth with minute punctae. Colpi are medium length and have a granular surface. Extensions of mesocolpia are present over the lalongate endoapertures. *Strephonema* (Fig. 19A, B) is subprolate in lateral view and circular to triangular in polar view. The surface is reticulate with large lumina which gradually decrease in size toward the margins of the mesocolpia. The large lumina are filled with rod-like, short elements, some of which are free standing while others extend diagonally and fuse with the muri. Colpi are long and wide with obtuse ends and a granular surface. Endoapertures are lalongate and elliptic.

Bucida (Fig. 21B), *Combretum laxum* (Fig. 20A), *C. farinosum* (Fig. 20B, C), *Conocarpus erecta* (Fig. 20E), *Lumnitzera* (Fig. 21C), *Quisqualis pellegriniana* (Fig. 21D), *Strephonema* (Fig. 21A), and *Terminalia edulis* (Fig. 20D) were examined with TEM. In general, the tectum is thick and the columellae are short, erect and simple. In *Q. pellegriniana,* some columellae appear to ramify into two or three straight, fine, very short segments just below the tectum. A well-developed infratectal granular layer is present in *Lumnitzera.* The foot layer is well developed in all taxa. It is either uniform in thickness (*C. farinosum, Strephonema, Lumnitzera*) or dome-shaped with the lower margin straight and the upper margin convex (*Bucida, T. edulis, C. laxum*). In *Conocarpus,* in some areas the foot layer is dome-shaped and in others it is thin and

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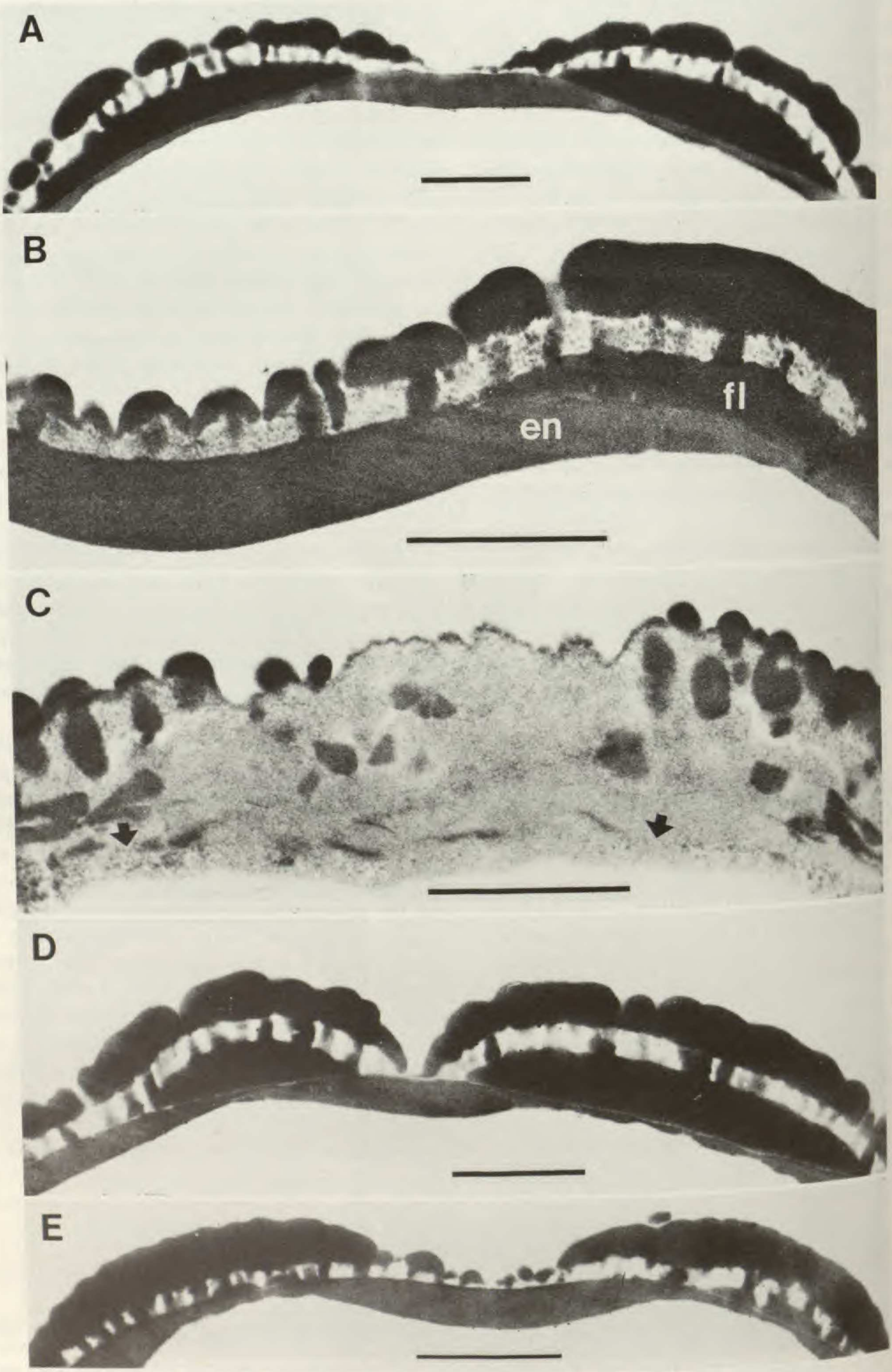
lumina.—C. *Poivrea coccinea.* Sublateral view. The circular endoaperture (dark area) is clearly evident through the ektexine. The colpus and subsidiary colpus membrane are granular. The surface is striate (cf. with striate surface of *G. senegalensis,* Fig. 18E).—D. *Lumnitzera racemosa.* Lateral view showing colpus with open endoaperture and two subsidiary colpi. The surface is rugulate. E, F. *Laguncularia racemosa.*—E. Lateral view. Colpi are narrow with a granular surface (subsidiary colpi are absent).—F. Surface detail near an open endoaperture. The surface is punctate. Scales equal 1 μm.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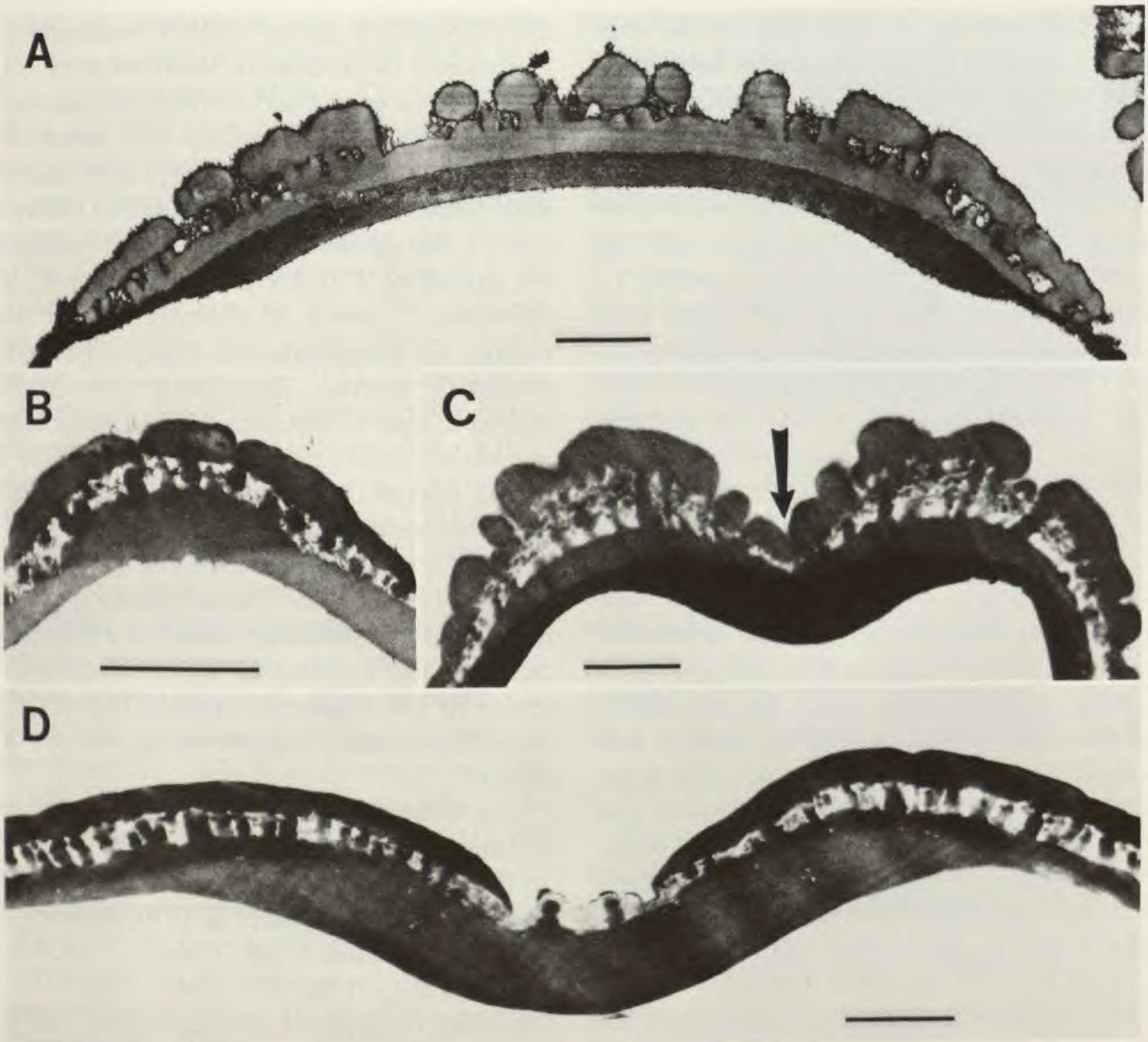

FIGURE 21. Transmission electron micrographs of Combretaceae pollen.—A. *Strephonema pseudocola.* Section of a mesocolpium. The thinning of endexine on both ends indicates the presence of endoapertures. The black outline of the ektexine is due to the precipitation of osmium.—B. *Bucida macrostachys.* Section of a mesocolpium between a colpus and a subsidiary colpus.—C. *Lumnitzera racemosa.* Section passing through two mesocolpia and an end of a subsidiary colpus (arrow). Note a thick infratectal granular layer.—D. *Quisqualis pellegriniana.* Section of a colpus and adjacent mesocolpia. Note the fine granular layer that covers the ektexinous processes on the colpus and extends into the intercolumellar spaces of the mesocolpia. Scales equal 1 μm.

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FIGURE 20. Transmission electron micrographs of Combretaceae pollen.—A. *Combretum laxum.* Section of two adjacent mesocolpia and a colpus or subsidiary colpus between them. Note the thick, dome-shaped foot layer. The endexine is thicker below the colpus (or subsidiary colpus) than below the mesocolpia. B, C. *Combretum farinosum.* Section through a portion of a mesocolpium (on the right) and a portion of a subsidiary colpus (on the left). Note the granular matrix between the columellae. In the subsidiary colpus the tectum is thin and discontinuous and the endexine (en) is greatly thickened. At the mesocolpial margin the thick foot layer (fl) tapers toward the subsidiary colpus.—C. Aperture region showing a thick, granular matrix covered by a fine membrane. Columellae are embedded in the matrix: the lower ends are free and the upper ends protrude as granules on the colpus surface. The foot layer appears to consist of fragmented lamellae. The endexine (arrows) is suggested by a slightly coarser, granular, narrow band at the lowermost margin.—D. *Terminalia edulis* (*Bernardo 23688*). Section includes two mesocolpia and the colpus or subsidiary colpus between them. Note the dome-shaped foot layer (identical to *C. laxum,* A). A "white line" separates the foot layer and endexine. The endexine is thick below the colpus or subsidiary colpus and thin elsewhere.—E. *Conocarpus erecta.* Section of two mesocolpia and the subsidiary colpus between them. Although the foot layer is thin and discontinuous in this section, other sections show it to be dome-shaped in the mesocolpia (similar to A and D). The striking dome-shaped foot layer in A and D is also present in Melastomataceae pollen (see Figs. 36–38). Scales equal 1 μm.

straight. The endexine is very thin in the mesocolpia, and thick at the colpi and subsidiary colpi. In *Strephonema,* it is either uniform or thin at the middle of the mesocolpia. At the margins of the mesocolpia near the subsidiary colpi, the foot layer usually terminates but sometimes appears to continue as a very fine layer over the endexine of the subsidiary colpi. In *T. edulis, C. laxum, Conocarpus,* and *Q. pellegriniana,* finer and shorter columellae and a thinner tectum are present in the subsidiary colpi region. In *C. laxum,* the endexine is granular near the endoaperture and granular-lamellate in *Conocarpus* and *T. edulis.*

Combretum farinosum (Fig. 20B, C) differs from the other three taxa examined with TEM in having a very fine granular matrix in the columellae layer. This matrix fills the spaces between the columellae and is also continuous in the subsidiary colpi region. Here, the columellae are shorter, the tectum is slightly thinner and often discontinuous as domes forming the granular and rugulate units on the exine surface. The granular matrix is also continuous in the colpi. The columellae are embedded in it with their protruding distal ends forming the granules of the colpus surface. The tectum appears as a thin film on the matrix (Fig. 20C). Irregular, broken lamellae of ektexinous material (foot layer?) are also present. The thick endexine also appears granular in the vicinity of the endoaperture and is difficult to distinguish from the granular matrix. In *Q. pellegriniana* (Fig. 21D) such a granular matrix is present over the thick endexine of the colpus. It extends into the intercolumellar spaces of the adjacent mesocolpia for a short distance, but is not as well developed as in *C. farinosum.*

Discussion

Apparently, there are no modern detailed studies of Combretaceae pollen (see Thanikaimoni, 1984). The following, therefore, is presented as a brief background of the basic morphology. Erdtman (1971) described *Quisqualis indica* as having colpi alternating with "pseudocolpoid thin walled areas" and made favorable comparisons with *Cacoucia, Combretum,* and *Terminalia.* He also described *Laguncularia racemosa* but did not mention the presence or absence of subsidiary colpi. *Quisqualis latialata* was described as having three pseudocolpi by Lobreau et al. (1969). Sowunmi (1973) described pollen of *Combretum glutinosum, Terminalia avicennioides, T. glaucescens, T. macroptera,* and *T. superba* in general as resembling each other and possessing a characteristic shape, aperture system, and exine. All grains were noted to have "colpoid streaks" (= subsidiary colpi) alternating with colpi. Lastly, Guers (1974) and Guers et al. (1971) also showed a fundamental similarity in the pollen of *Combretum aculeatum, C. grandiflorum, C. lokele, C. micranthum, C. platypterum, C. smeathnianni, Conocarpus erectus, Pteleopsis diptera, Terminalia glaucescens, T. laxiflora,* and *T. superba.* All had colpi alternating with subsidiary colpi. The one SEM illustrated, that of *Combretum aculeatum,* is similar to *C. cacoucia* (Fig. 15A–C).

From a comparative point of view, Erdtman (1971: 117) felt that "Pollen grains ± similar to those in Combretaceae occur in Melastomataceae (cf. also Lythraceae and Penaeaceae). The grains in Haloragaceae, Hernandiaceae, Myrtaceae, Punicaceae, Sonneratiaceae, etc. are ± different."

Our SEM observations indicate several rather distinctive groups. *Combretum* (Figs. 15A–C, 16D–G), *Quisqualis* (Figs. 15F, 16H, I), *Bucida* (Fig. 17A), *Conocarpus* (Fig. 17B), *Pteleopsis* (Fig. 17C), *Terminalia* (Figs. 16A–C, 17D, F), *Ramatuella* (Fig. 17E, G), *Guiera* (Fig. 18E), *Poivrea* (Fig. 19C), and *Lumnitzera* (Fig. 19D) comprise the first group and are similar in having colpi alternating with subsidiary colpi. Various surface patterns are repersented in this group. A second group, characterized by the presence of an echinate surface and subsidiary colpi is represented by *Thiola* (Fig. 15D, E) and *Anogeissus* (Fig. 18D, F). A third group, consisting only of *Buchenavia* (Fig. 18A–C) has an echinate surface but lacks subsidiary colpi. A fourth group, also consisting of just one taxon, *Laguncularia* (Fig. 19E, F), has a punctate surface and lacks subsidiary colpi. The fifth group, represented only by *Strephonema* (Fig. 19A, B), also lacking subsidiary colpi, is completely different from all other Combretaceae in having a reticulate surface. Interestingly, this reticulate surface has not been observed in any other member of the Myrtales core families. In contrast to the diverse surface morphology are the TEM data which indicate structural similarities. However, these data are limited at present. *Strephonema* is so distinct from all other members of Combretaceae that it might best be considered to constitute a separate subfamily Strephonematoideae, as suggested by Dahlgren and Thorne (1984) and others.

Generalized comparisons with pollen from the core families essentially agree with Erdtman's (1971) suggestions given above. The pollen included in our first group shows broad resemblances to some Penaeaceae, some Melastomataceae, and some Crypteroniaceae. Genera of Penaeaceae with these resemblances are: *Endonema* (Fig. 25A, C), *Brachysiphon* (Figs. 24A, B, 25D), and *Sonderothamnus* (Fig. 25E). Genera of Melastomataceae that show these resemblances are: *Memecylon* (Fig. 31E), *Mouriri* (Fig. 31F), *Trembleya* (Fig. 32A), *Osbeckia* (Fig. 32B), *Tibouchina* (Fig. 32C), *Tristemma* (Fig. 32D), *Votomita* (Fig. 32E), *Marumia* (Fig. 33A), *Dissotis* (Fig. 33C, D), *Acanthella* (Fig. 33E), and *Dissochaeta* (Fig. 33F). Genera of Crypteroniaceae that show these resemblances are *Axinandra* (Fig. 28B) and *Dactylocladus* (Fig. 28A, C, E). The other four groups do not, at least to this time, show resemblances to other Myrtales. In TEM, the very markedly domed foot layer of Combretaceae (Fig. 20A, B, D, F) was recognized also in Melastomataceae (*Tristemma,* Fig. 37A; *Trembleya,* Fig. 37B; *Osbeckia,* Fig. 37D, E; *Marumia,* Fig. 38A), and Penaeaceae (*Penaea,* Fig. 26A; *Sonderothamnus,* Fig. 26B; *Glischrocolla,* Fig. 27A; *Stylapterus,* Fig. 27E). Furthermore, the entire exine structure of *Lumnitzera* compares favorably with that in Penaeaceae (*Glischrocolla,* Fig. 27A).

ALZATEACEAE

In *Alzatea verticillata,* the only member of this monotypic family, pollen is tricolporate, radially symmetrical, isopolar, spheroidal to subprolate in lateral view, hexagonal to triangular (goniotreme with obtuse corners and straight sides) in polar view (Fig. 4B, D). The surface is psilate except in the elliptical areas at the middle of the mesocolpia where it is psilate-punctate; these areas are slightly depressed and possibly represent subsidiary colpi or intercolpar concavities. Colpi are long, with obtuse ends, and a smooth surface. A wide, coarse margin is present around the colpus. Endoapertures are lalongate. Extensions of the mesocolpia are present over the endoapertures.

On the sides of the mesocolpia (i.e., around the punctate, elliptic areas) the foot layer is well developed in the form of continous "hills" or "domes" (Fig. 6B). The thick tectum has a smooth, slightly undulating upper margin. Its lower margin corresponds in shape to that of the foot layer, resulting in an undulated or a zig-zag columellae layer between the tectum and the foot layer. The short, erect columellae are unbranched. The endexine is relatively thin. At the middle of the mesocolpia (Fig. 6C), where the surface is punctate, the exine becomes thinner: the foot layer at first becomes thinner and then is present only as wide bases of the columellae; the columellae slightly increase in height and become branched; and the thin tectum has large perforations and an infratectal granular layer. The endexine increases in thickness as it does in taxa with subsidiary colpi.

Near the colpi, the endexine is very thick and the foot layer tapers and is present either as a thin layer or is absent. At the margins of the mesocolpia, the very short columellae and the thin tectum with an infratectal granular layer are present on this thick endexine. The endexine is granular in the vicinity of the endoapertures.

Discussion

The punctate areas at the middle of the mesocolpia in *Alzatea* are suggested as being incipient subsidiary colpi by Muller (1975). The exine indeed is thinner in this area as is shown in the TEM (Fig. 6C). As mentioned by Muller, *Alzatea* pollen is comparable with that of those species of *Rotala* that show indistinct subsidiary colpi (Guers, 1970). Pollen of this genus has been characterized as (1) three colporate, (2) three colporate with indistinct subsidiary colpi, and (3) three colporate with distinct subsidiary colpi (Guers, 1970). Further, a spectrum of heterocolpateness also occurs within a single species (Cos Campos, 1964). *Alzatea* pollen may also be compared with *Physocalymma* (Cos Campos, 1964; van Campo in Lourteig, 1965). A detailed examination involving electron microscopy of these two lythraceous genera (i.e., *Rotala* and *Physocalymma*) should be instructive.

Alzatea has been treated in several taxonomic systems (see Dahlgren & Thorne, 1984). Muller (1975) treated it in Crypteroniaceae following the system of van Beusekom-Osinga and van Beusekom (1975), as an ancestral tricolporate type, deriving from it the bisyncolporate bilateral *Crypteronia* type and the heterocolporate triradiate *Dactylocladus* type. In a sense, he considered *Alzatea* to have the relatively unspecialized pollen common in some angiosperm families, particularly in Lecythidaceae, Rhizophoraceae, Combretaceae, and Lythraceae (including Pun-

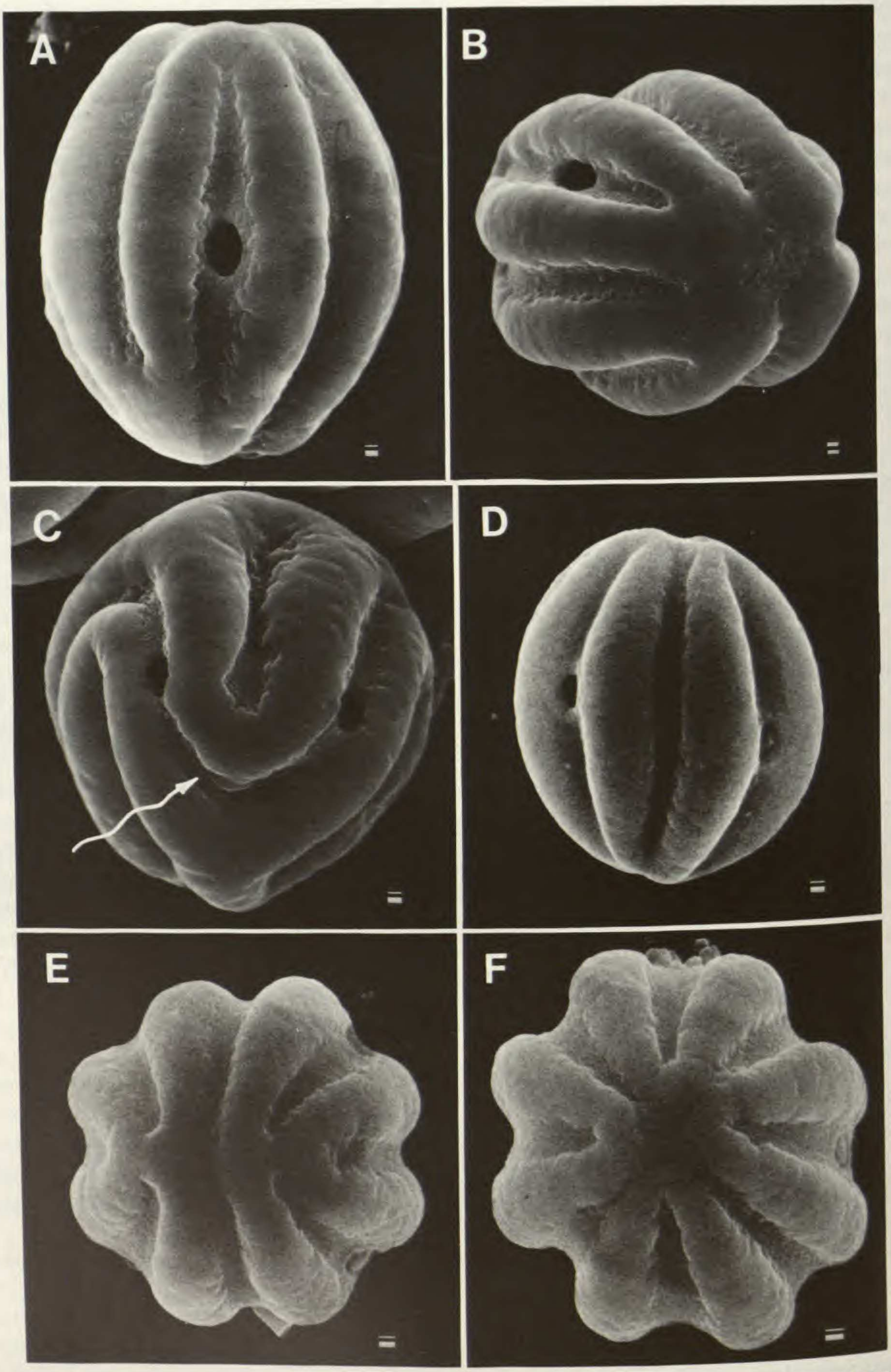

FIGURE 22. Scanning electron micrographs of Penaeaceae pollen. A–C. *Penaea mucronata*.—A. Lateral view with colpus at center. Note the irregular development of the subsidiary colpi. The subsidiary colpus at the left appears to unite with other subsidiary colpi at the top pole while at the bottom pole it is free. The subsidiary colpus at the right appears to unite with subsidiary colpi at both poles (see also Fig. 25E). The exine surface is psilate; in the colpus and subsidiary colpus it is granular.—B. Subpolar view showing portions of four colpi alternating with four subsidiary colpi. Note the patch of granular exine at the pole. See also scanning electron micrograph of Dahlgren (1971, fig. 2).—C. Sublateral view showing colpi united to form an undulating syncolpus (arrow). Note the two circular endoapertures as well as fused subsidiary colpi (i.e., "synsubsidiary colpi"). D–F. *Stylapterus ericoides*.—D. Lateral view with a subsidiary colpus at center. Grains similar to C of *P. mucronata*

icoideae, and in Lythroideae particularly *Adenaria, Pemphis, Pehria, Pleurophora, Physocalymma, Woodfordia,* and some *Rotala*).

Although the pollen of *Alzatea* is generalized, we feel that it is very similar to that of Chrysobalanaceae (Patel et al., 1983a) in shape as well as in surface features. Endomorphically, it is similar to *Dactylocladus, Axinandra,* and Chrysobalanaceae (see also Corynocarpaceae, Nowicke & Skvarla, 1983) in having a zigzag columellae layer.

RHYNCHOCALYCACEAE

Rhynchocalyx lawsonioides was examined with both SEM (Fig. 4A, C) and TEM (Fig. 6D). Pollen is tricolporate, heterocolpate with three subsidiary colpi, radially symmetrical and isopolar, spheroidal in lateral view and triangular-hexagonal in polar view. The surface is coarse, with many punctae and irregular channels. Colpi are long, narrow with acute ends, and have a granular surface. Endoapertures are lalongate. Mesocolpial extensions are present over the endoapertures. Subsidiary colpi are wide and in some grains they appear to be united at the poles. Their surface is similar to that of the mesocolpia. Thin section (Fig. 6D) shows the foot layer to be well developed in the mesocolpial regions; columellae are numerous, erect, and branched distally, often forming an infratectal granular layer (see Muller, 1975). The tectum is thick, perforate, with an undulating upper margin that is locally discontinuous and separated into domes. The endexine is very thin and has an irregular lower margin. At the colpi and subsidiary colpi the endexine is thick, columellae are shorter, and the tectum and foot layer are thinner than in the mesocolpial areas. In the region of the endoaperture, the endexine is granular, the foot layer is tapered and the shorter columellae and thin tectum lie directly on the endexine. Additional comments regarding *Rhynchocalyx* pollen can be found in the discussion of Lythraceae and Crypteroniaceae.

PENAEACEAE

Pollen grains are tricolporate in *Brachysiphon rupestris* (Fig. 25D), *B. fucatus* (Fig. 24B), *Endonema laterifolia* (Fig. 25A, C), *Sonderothamnus petraeus* (Fig. 25E), *S. speciosus* (Fig. 24F), and *Saltera sarcocolla* (Fig. 24C, D). They are tetracolporate in *Penaea cneorum* (Fig. 23B, D), *P. mucronata* (Fig. 22A–C), and *Stylapterus ericoides* (Fig. 22D–F), and 5-colporate in *Glischrocolla formosa* (Fig. 23A, C). Some tetracolporate grains were also present in *Brachysiphon fucatus* (Fig. 24A), *Glischrocolla,* and *Sonderothamnus speciosus,* whereas 6-colporate grains were observed in *Saltera* (Fig. 24E). Pollen of these taxa are heterocolpate with isomerous subsidiary colpi or intercolpar concavities (in *Saltera* and *Glischrocolla*) alternating with colpi. They are radially symmetrical, isopolar (except some in *Penaea, Saltera,* and *Stylapterus,* see below), spheroidal to subprolate in lateral view, and circular to hexagonal (in tricolporate species) or circular to octagonal (in tetracolporate species) in polar view. The surface is psilate in *Penaea, Brachysiphon, Saltera, Glischrocolla, Sonderothamnus,* and *Stylapterus,* with few pits and punctae. In *Endonema* it is rugulate with punctae.

Colpi are long, with acute (*Brachysiphon rupestris, Penaea, Saltera,* and *Stylapterus*) or obtuse (*Endonema, B. fucatus, Glischrocolla, Sonderothamnus*) ends, the pollen surface is granular with the exception of *Brachysiphon rupestris, Sonderothamnus speciosus,* and *Saltera,* where it is smooth. Asymmetric colpi similar to those in *Olinia* were common in *Glischrocolla* (Fig. 23C), *Saltera* (Fig. 24D), and *Sonderothamnus* (Fig. 24F). Endoapertures in such grains are located either on the equator, or on one polar face. The shape of these grains is spherical except in *Saltera* which also has some ovoidal, heteropolar grains. Endoapertures are circular in *Penaea* and *Stylapterus,* and lalongate-elliptic with two lateral extensions in *Endonema* (Fig. 25B) and *Brachysiphon.* In *Endonema,* extensions of the mesocolpia are present over the endoapertures. They are either very small or absent in *Brachysiphon* and are absent in the remaining taxa. In *Sonderothamnus* and *Saltera,* the endoapertures are slightly elliptic-lalongate and in *Sonderothamnus petraeus* (Fig. 25F) the colpus membrane often persists as a horizontal bar over the

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also occur in *S. ericoides* but are not herein illustrated.—E,F. Polar views. Four colpi alternate with four subsidiary colpi. The subsidiary colpi are united at the poles in various combinations. For example, in E the two opposite subsidiary colpi are united while in F all four are united. The exine is smooth with few punctae and channels. Scales equal 1 μm.

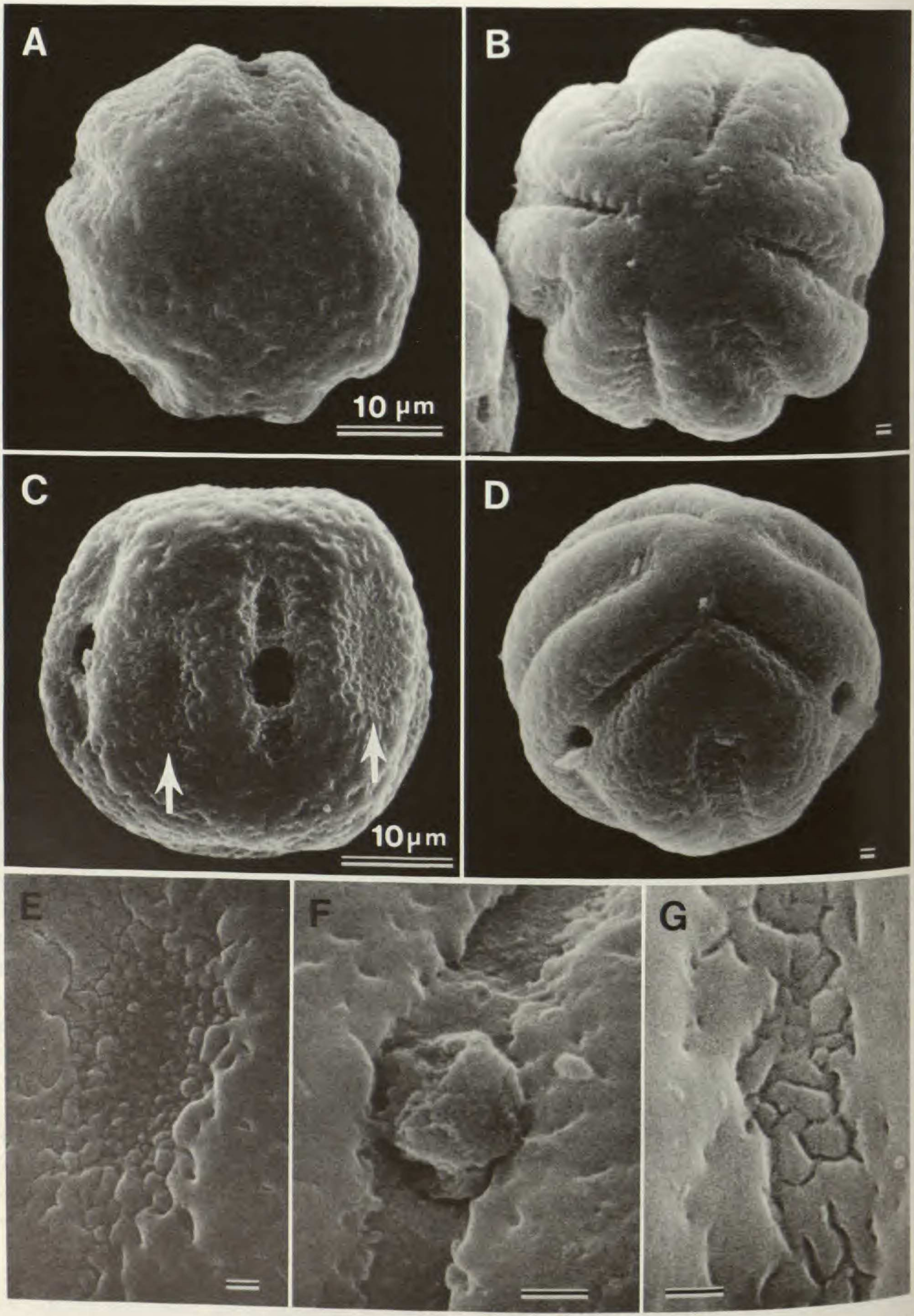


FIGURE 23. Scanning electron micrographs of Penaeaceae pollen. A, C, E. *Glischrocolla formosa.*—A. Polar view.—C. Lateral view. Note the difference in the size and position of the two visible intercolpar concavities (arrows). The central colpus is slightly asymmetric.—E. Details of an intercolpar concavity showing rugulate margin and granular center. B, D, F. *Penaea cneorum.* subsp. *cneorum.*—B. Polar view. Compare with *Quisqualis* (Fig. 16I).—D. Subpolar view of a grain with united colpi. Note the opercula near the endoapertures.—F. A circular endoaperture which is covered by an operculum.—G. *Sonderothamnus speciosus.* Rugulate surface of a sibsidiary colpus. Compare with Oliniaceae (Fig. 13D). Unless otherwise indicated, scales equal 1 µm.

open endoapertures. Round opercula were observed in *Penaea cneorum* (Fig. 23F), *Brachysiphon fucatus* (Fig. 24A), *Saltera*, and *Stylapterus*.

The subsidiary colpi are long and have a smooth to granular surface except in *Endonema* (granular-verrucate) and *Sonderothamnus* (rugulate and similar to *Olinia*). The intercolpar concavities of *Saltera* and *Glischrocolla* have a rugulate surface on the margin and become granular toward the center. Subsidiary colpi are often united in *Brachysiphon* and *Sonderothamnus*. Heteropolar grains with colpi or subsidiary colpi or intercolpar concavities united in various configurations were observed in *Penaea* (Figs. 22C, 23D), *B. fucatus* (Fig. 24A), *Saltera*, and *Stylapterus* (Fig. 22E, F). In *Saltera*, 6-colporate grains with five intercolpar concavities and three very small, rudimentary or incipient (?) colpi were observed (Fig. 24E). In *Sonderothamnus speciosus* some grains appear to be fused in random configurations.

In TEM (Figs. 26, 27), the tectum along the mesocolpia is very thick and without perforations in all taxa except *Glischrocolla* (Fig. 27A). A thin infratectal granular layer is present in all taxa except *Penaea* (Figs. 26A, 27F). The foot layer is also prominent, usually thicker than the tectum and dome-shaped. The upper margin of the foot layer is irregular. Between it and the tectum, problematical columellae are usually distinguishable. They are thick, very short and irregular and often surrounded by the infratectal granular layer. This columellae layer is undulating or zig-zag in *Saltera* (Fig. 27C, D), and slightly so in *Brachysiphon acutus* and *Sonderothamnus* (Fig. 26B); in *Penaea* (Figs. 26A, 27F), it is represented by a very thin, undulating gap between the tectum and foot layer.

Toward the colpi and subsidiary colpi or intercolpar concavities, the endexine increases in thickness while the foot layer and tectum decrease. In the subsidiary colpus region in *Sonderothamnus* (Fig. 26C) and *Brachysiphon acutus* (Fig. 27B), a fragmented, thin foot layer supports an elaborate granular, spongy layer. This granular layer is a continuation of the infractectal layer of the mesocolpia but is much wider and better developed here. The intercolpar concavity of *Glischrocolla* and *Saltera* also has such a layer but it is not as thick as in the above two taxa. The spongy granular layer is covered by a thin tectum. In *Stylapterus* and *Penaea*, the tectum, granular layer, and foot layer are all very thin in the subsidiary colpi. The endexine is very thick and granular near the endoaperture.

Discussion

Pollen of the seven genera constituting Penaeaceae are best known through the light microscope studies of Dahlgren (1967a, 1967b, 1967c, 1968, 1971) as part of his comprehensive study of the family. While variations in pollen size and shape are common the pollen is fairly uniform and is characterized by colpi alternating with subsidiary colpi. The only major difference is in the number of apertures which seem to be the most variable in *Penaea* and *Saltera* (Dahlgren, 1968, 1971). These observations are also supported in other studies (i.e., Erdtman, 1971; Archangelsky, 1971).

Our results indicate that exomorphically, Penaeaceae pollen resembles that of Oliniaceae (see Oliniaceae discussion), Melastomataceae (compare *Endonema*, Fig. 25A, C, with *Tristemma*, Fig. 32D, and *Dissotis*, Fig. 33C, D) and Combretaceae (compare *Brachysiphon*, Fig. 25D, with *Combretum*, Fig. 15B, and *Quisqualis*, Fig. 16I, with *Penaea*, Fig. 23B). Endomorphically, the exine structure in the mesocolpium is similar to that of Oliniaceae (Fig. 14B–E) while the subsidiary colpal areas show a somewhat distant similarity to Onagraceae pollen (compare *Sonderothamnus*, Fig. 26C, with Figs. 60–63).

CRYPTERONIACEAE

Crypteronia paniculata (Figs. 30B, 31B–D), *Dactylocladus stenostachys* (Figs. 28A, C, E–G, 29), and *Axinandra zeylanica* (Figs. 28B, D, 30C) were examined with SEM and TEM. *Crypteronia* sp. (Fig. 31A) was examined only with SEM and *C. leptostachys* (Fig. 30A) only with TEM. *Crypteronia* (Fig. 31A–D) pollen is dicolporate, syncolpate, and bilaterally symmetrical. It is shaped like a football with the two endoapertures situated at the opposite pointed ends. It is elliptic in polar view and in lateral view (away from the endoapertures, or facing the mesocolpium); and circular to square in lateral view facing the endoaperture. The colpi have a smooth surface. They are united at both poles forming a circle around the grain. The endoapertures are lalongate, elliptic. The surface of the mesocolpia is rugulate. At the middle of each mesocolpium there is an equatorially elongated intercolpar concavity which has a verrucate-rugulate surface.

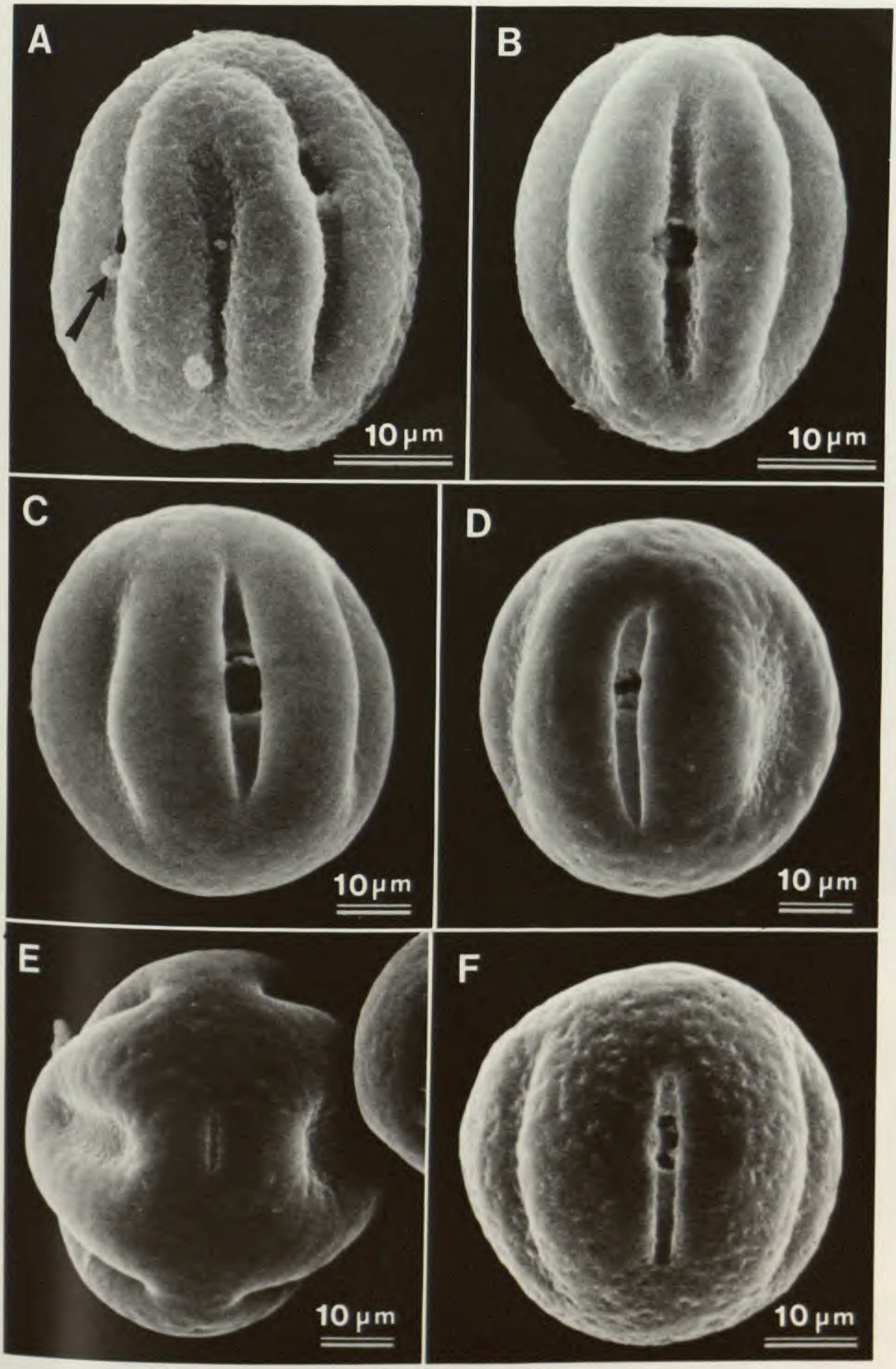
Dactylocladus and *Axinandra* both have tricolporate (rarely tetracolporate in *Dactylocladus*), heterocolpate, radially symmetrical, isopolar pollen (Fig. 28). Pollen is spheroidal in lateral view and triangular-hexagonal in polar view. In *Axinandra,* the surface of the mesocolpia is psilate, with a few scattered punctae. The colpi have acute ends, a smooth appearing surface, and are narrower than those in *Dactylocladus.* The obscure endoapertures are covered by exine extensions of the mesocolpia. The subsidiary colpi are long and sometimes united at the poles. Often, they are wide, appearing like intercolpar concavities. Their surface is punctate. The margin of the mesocolpia around the subsidiary colpi is often more punctate than other areas of the pollen grain. In *Dactylocladus,* the surface is psilate with some punctae and channels on the mesocolpia around the subsidiary colpi. The colpi are wide with a granular surface and obtuse ends which are sometimes united in tetracolporate grains. The obscure endoapertures are slightly protruding and have extensions of the mesocolpia over them. The subsidiary colpi are wide, with a granular surface, and irregular channels. At the poles the subsidiary colpi are united.

The exine of *Crypteronia* is thin (Fig. 30A, B). The narrow and more or less uniform tectum and foot layer are separated by short, thick, and simple (unbranched) columellae. The endexine is thick below the colpi and intercolpar concavities but thin elsewhere. It is granular-lamellate near the endoapertures. In contrast, the exine of *Dactylocladus* (Fig. 29A–C) is thick. It has a thick tectum and a broad foot layer which is often dome-shaped (Fig. 29B, mesocolpium to the left). A narrow columellae layer with thin, short columellae separates the tectum and foot layer. In some parts of the grain, the columellae layer follows a zig-zag pattern. The endexine is thick be-

FIGURE 24. Scanning electron micrographs of Penaeaceae pollen. A, B. *Brachysiphon fucatus.*—A. Lateral view of a tetracolporate syncolpate grain. Note that the two visible endoapertures are not on the same horizontal plane. Arrow indicates an operculum.—B. Lateral view of a tricolporate grain. C–E. *Saltera sarcocolla.*—C. Lateral view. The endoaperture is on the equatorial plane and the colpus is symmetrical.—D. Lateral view. Note the asymmetrical colpus with a short and a long segment. The endoaperture is above the equatorial plane. The surface of the intercolpar concavities is granular.—E. Many grains with abnormal number of colpi and intercolpar concavities were noted, such as this one with six colpi, five intercolpar concavities, and three rudimentary or incipient (?) colpi. Fusion of the exines of grains was also present.—F. *Sonderothamnus speciosus.* Lateral view. Note the asymmetric colpus and the endoaperture situated above the equator. Scales equal 10 μm.

FIGURE 25. Scanning electron micrographs of Penaeaceae pollen. A–C. *Endonema lateriflora.*—A. Lateral view. The surface is rugulate while the subsidiary colpus has a verrucate-granular surface.—B. Elliptic, lalongate endoaperture as viewed from the inside of the pollen grain. The arrows show two lateral extensions of the endoaperture.—C. Polar view showing three colpi and three subsidiary colpi. Extensions of the mesocolpia are evident over the endoapertures.—D. *Brachysiphon rupestris.* Lateral view with a colpus at the center and two subsidiary colpi. The exine surface is psilate while the subsidiary colpus is granular. E, F. *Sonderothamnus petraeus.*—E. Lateral view with colpus at center and adjacent subsidiary colpi. At the lower pole the two visible subsidiary colpi and presumably the subsidiary colpus at the back of the pollen grain appear to be united. At the upper pole the subsidiary colpus to the left is not united with other subsidiary colpi (see also Fig. 22A).—F. View of colpus. An ektexinous bar over the endoaperture gives the impression of two pores being present within each colpus. Ektexinous bars are also common in some Melastomataceae pollen (see Figs. 32B, C, 33A, C, D). The surface of the mesocolpia is psilate with few pits and channels while the colpus (and subsidiary colpus of E) is granular. Scales equal 1 μm.

FIGURE 26. Transmission electron micrographs of Penaeaceae pollen.—A. *Penaea mucronata.* Section of a mesocolpium with an endoaperture (arrow) on the left and a subsidiary colpus on the right. A very thin undulating electron translucent "line" separates the thick tectum from the thick foot layer. Near the endoaperture, both layers are thin and discontinuous; over the subsidiary colpus they are extremely thin. The endexine is relatively thin in the middle of the mesocolpium and thick near the subsidiary colpus and endoaperture. In the latter area it is also granular. B, C. *Sonderothamnus petraeus.*—B. Section of a mesocolpium. The thick tectum is imperforate. An infratectal granular layer is partially obscured by osmium precipitate. The foot layer is much thicker than the tectum. The endexine is thin and relatively uniform.—C. Section of a subsidiary colpus. The tectum is thin with a wavy or lobed outer margin. The infratectal layer is well developed. Immediately below, the foot layer (arrow) appears to be highly disrupted or fragmented. There are no distinguishable columellae. The endexine (en) is as thick or thicker than the ektexine. This section is reminiscent, in a sense, to sections of Onagraceae (see Figs. 60–63).—D. *Sonderothamnus speciosus.* Section of a mesocolpium near a subsidiary colpus (on the right). Compare with B and C. The exine sections represented in Figure 26 should be compared with Oliniaceae sections in Figure 14. Scales equal 1 μm.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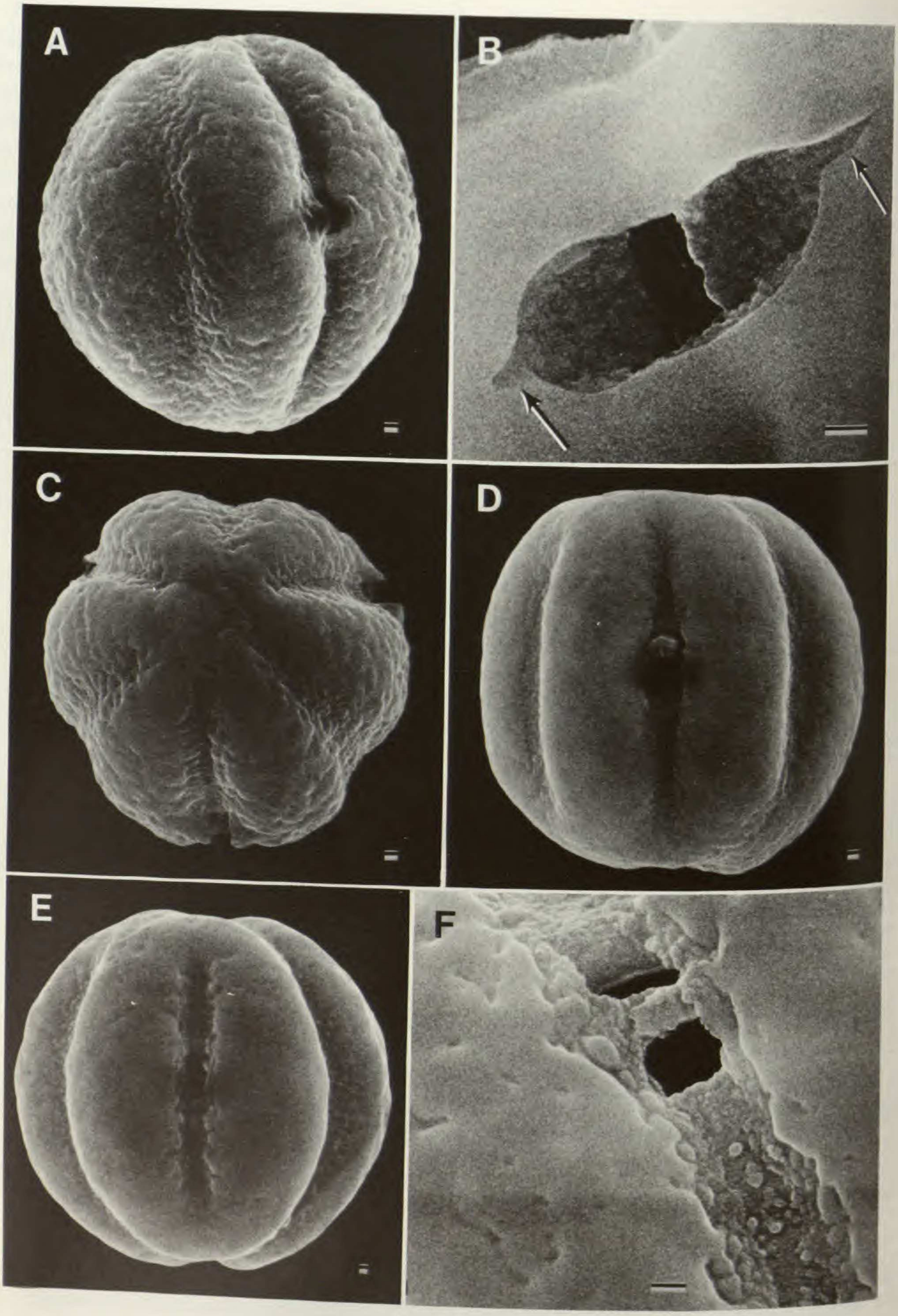
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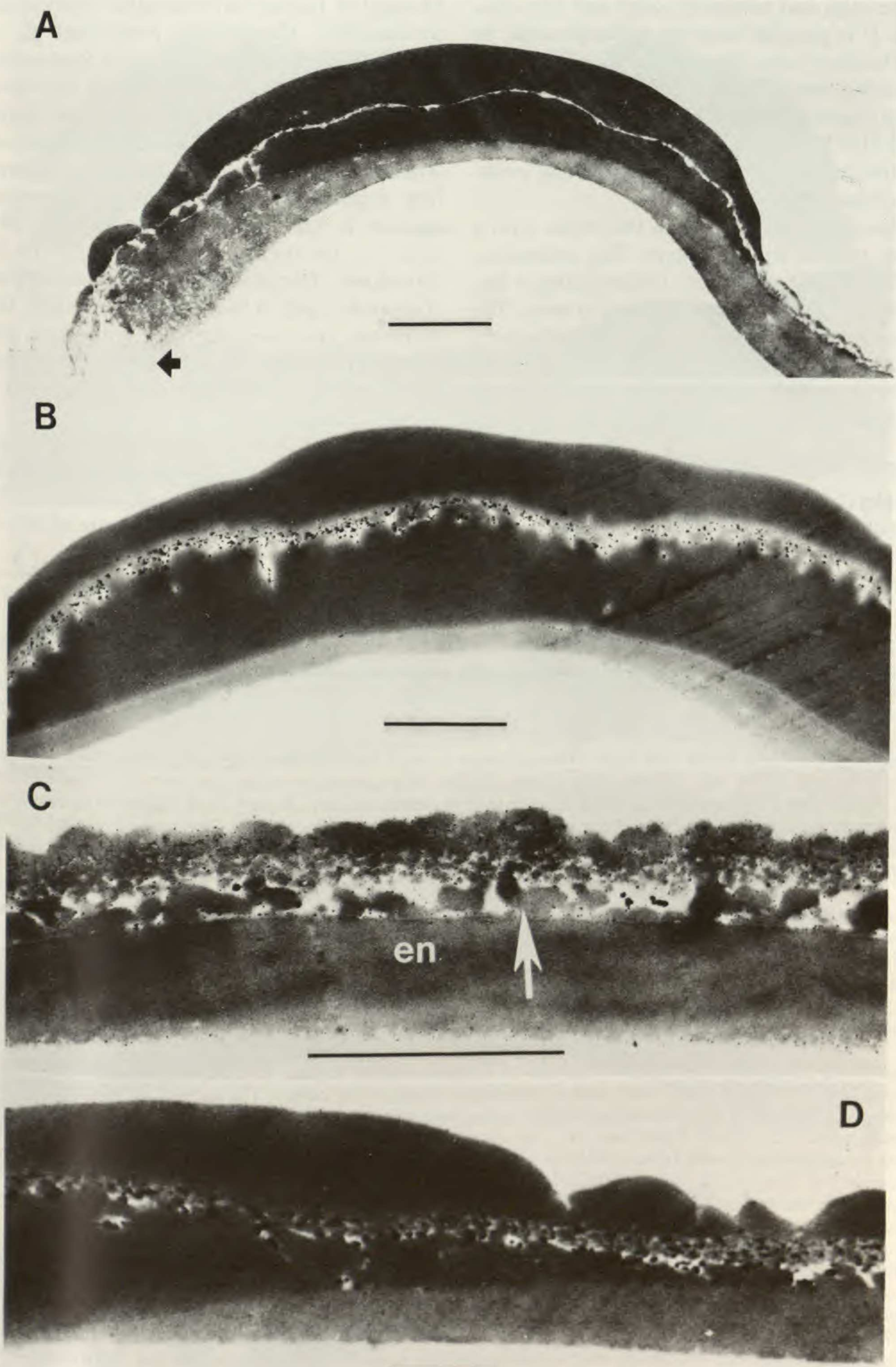
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low the colpi and subsidiary colpi and thin elsewhere. It is granular near the endoapertures. In the subsidiary colpi the tectum, foot layer, and columellae become very thin. In our TEM, we did not clearly recognize the small granules which Muller (1975) described as best developed on the lower tectum surface of *Dactylocladus* and weakly developed on *Crypteronia*.

Axinandra (Fig. 30C) has a thin exine with a narrow tectum and foot layer. The columellae are thick or thin and short. Occasionally, a zigzag pattern of the columellae layer is seen. The endexine is thick below the colpi and subsidiary colpi, thin elsewhere, and granular near the endoapertures. In the subsidiary colpi the tectum and foot layer are narrow and the columellae are short.

Discussion

Muller (1975) described with light and electron microscopy (SEM and TEM) the pollen morphology of *Axinandra beccariana, Dactylocladus stenostachys, Crypteronia paniculata, C. cumingii, C. griffithii, Rhynchocalyx lawsonioides,* and *Alzatea verticillata.* The latter two species are treated now as separate monotypic families (i.e., *Rhynchocalyx* in Rhynchocalycaceae, and *Alzatea* in Alzateaceae). As discussed previously (see Alzateaceae), three pollen types were recognized in the Crypteroniaceae (Muller, 1975: 276) ". . . the tricolporate *Alzatea*-type, the heterocolpate *Dactylocladus*-type (*Dactylocladus, Axinandra,* and *Rhynchocalyx*) in which three colporate apertures alternate with three pseudocolpi, and the bisyncolporate *Crypteronia*-type." The less specified *Alzatea*-type was regarded as ancestral in the family.

In a general sense, we are in complete agreement with Muller (1975) that *Axinandra* and *Dactylocladus* pollen compare with pollen in Melastomataceae (see dicolporate grain of *Miconia*

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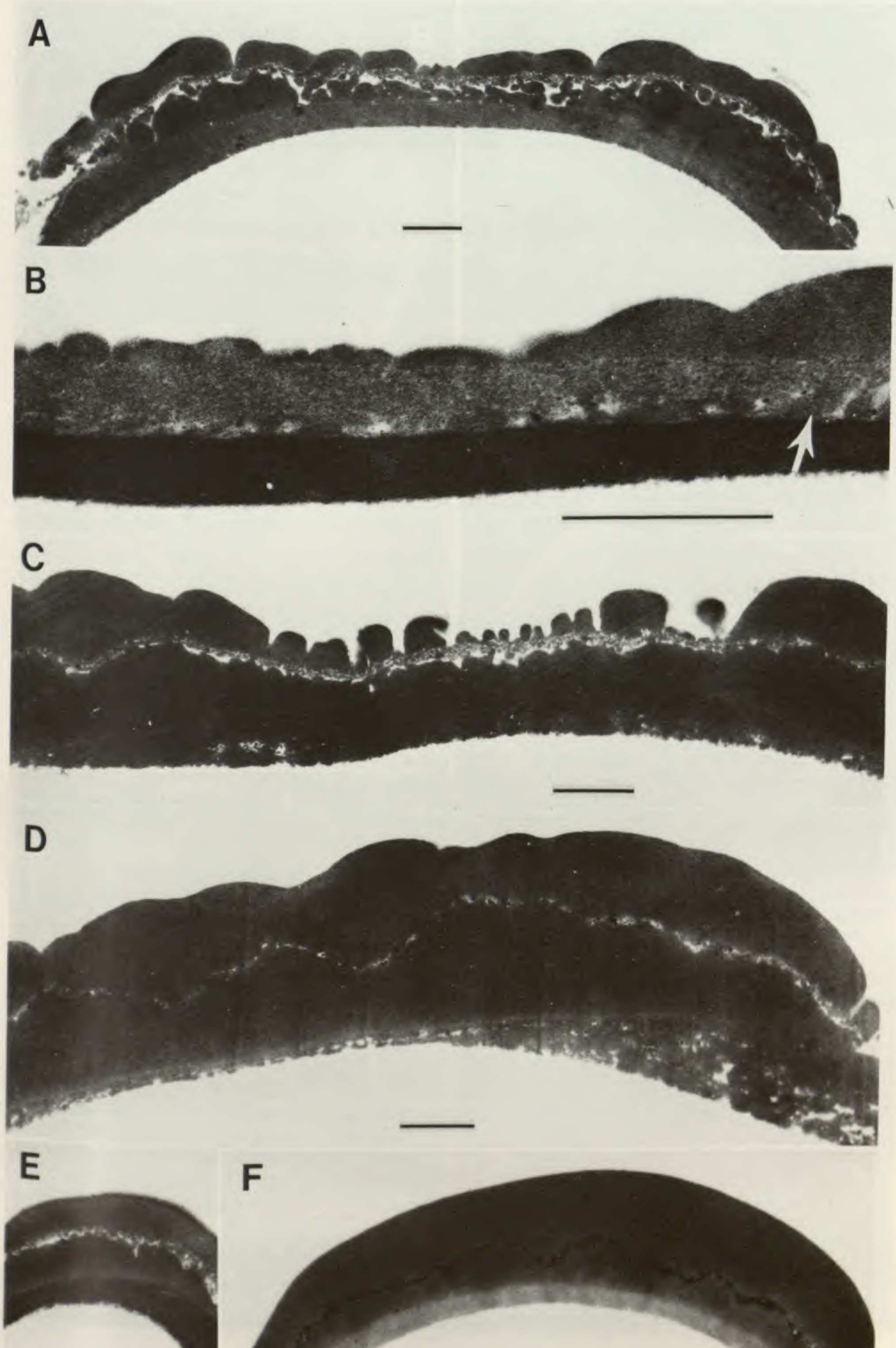
FIGURE 27. Transmission electron micrographs of Penaeaceae pollen.—A. *Glischrocolla formosa.* Section of two mesocolpia and an intercolpar concavity (center). The outer margin of tectum appears lobed due to the punctae of the surface. A thin and uniform infratectal granular layer is present in the mesocolpia and the intercolpar concavity. The foot layer is dome-shaped in the mesocolpia. Its upper margin is wavy and irregular. In the intercolpar concavity, it is thin and highly disrupted. It is difficult to distinguish columellae due to the irregular upper margin of the foot layer. The endexine is thick and uniform becoming thicker below the colpi (extreme left and right).—B. *Brachysiphon acutus.* Section of a subsidiary colpus and part of a mesocolpium (at right). Note a thin tectum which becomes thicker over the mesocolpium. A very thick infratectal granular layer is present in the subsidiary colpus which is reduced slightly in the mesocolpium. The well-developed endexine is stained darker than the ektexine layers. Between the endexine and the infratectal granular layer irregular, disrupted ektexinous elements (arrow) are present, which could be either columellae or fragments of the foot layer, or both. In the mesocolpium, however, distinct columellae and well-developed, dome-shaped foot layer (not included here) are present. C, D. *Saltera sarcocolla.*—C. Section of an intercolpar concavity and adjacent mesocolpia.—D. Section of a mesocolpium. Note the undulating columellae layer between the very thick tectum and foot layer. The colpus is to the right and the endexine increases in thickness toward the right.—E. *Stylapterus ericoïdes.* Section of a mesocolpium.—F. *Penaea cneorum* subsp. *ruscifolia.* Section of an entire mesocolpium. Note that the very thick tectum and foot layer are separated by an undulating gap (columellae layer), which appears dark due to osmium precipitate. Scales equal 1 μm.

FIGURE 28. Scanning electron micrographs of Crypteroniaceae pollen. A, C, E–G. *Dactylocladus stenostachys.*—A. (*SPH 3975*). Lateral view with a subsidiary colpus at the center. The subsidiary colpi are united at the poles. Compare also with scanning electron micrograph of Muller (1975, Pl. IV, figs. 1–3).—C. (*Chai,* 1982). Subpolar view.—E. (*732A*). Polar view of a tetracolporate grain.—F. (*SPH 3975*). Subpolar view of a tetracolporate, syncolpate grain.—G. (*Chai,* 1982). A subsidiary colpus with rugulate surface. B, D. *Axinandra zeylanica* (*Gunatilleke & Gunatilleke 582*).—B. Lateral view. Endoaperture is covered by colpus membrane.—D. Fused grains were occasionally noted in this collection. Rugulate surface of the subsidiary colpi of both grains is visible. Scales equal 1 μm.

FIGURE 29. Transmission electron micrographs of Crypteroniaceae pollen. A–C. *Dactylocladus stenostachys.*—A. (*Chai,* 1982). Section of an entire grain cut in plane that includes two colpi (arrows) and one subsidiary colpus. Note that the thin columellae layer has a distinct zig-zag configuration in some portions of the exine.—B. (*Chai 39708*). Section showing two mesocolpia and a subsidiary colpus between them. The mesocolpium on the right shows a zig-zag columellae layer which is straight in the mesocolpium on the left. Arrow indicates an endoaperture.—C. (*SPH 3975*). Same as above but a distinct zig-zag columellae layer is not visible. In the subsidiary colpus, thin tectum, fine columellae, and a very thin foot layer are present. Note the increase in the thickness of the endexine below colpi and subsidiary colpus. Arrow indicates an endoaperture where the endexine is lamellated. Scales equal 1 μm.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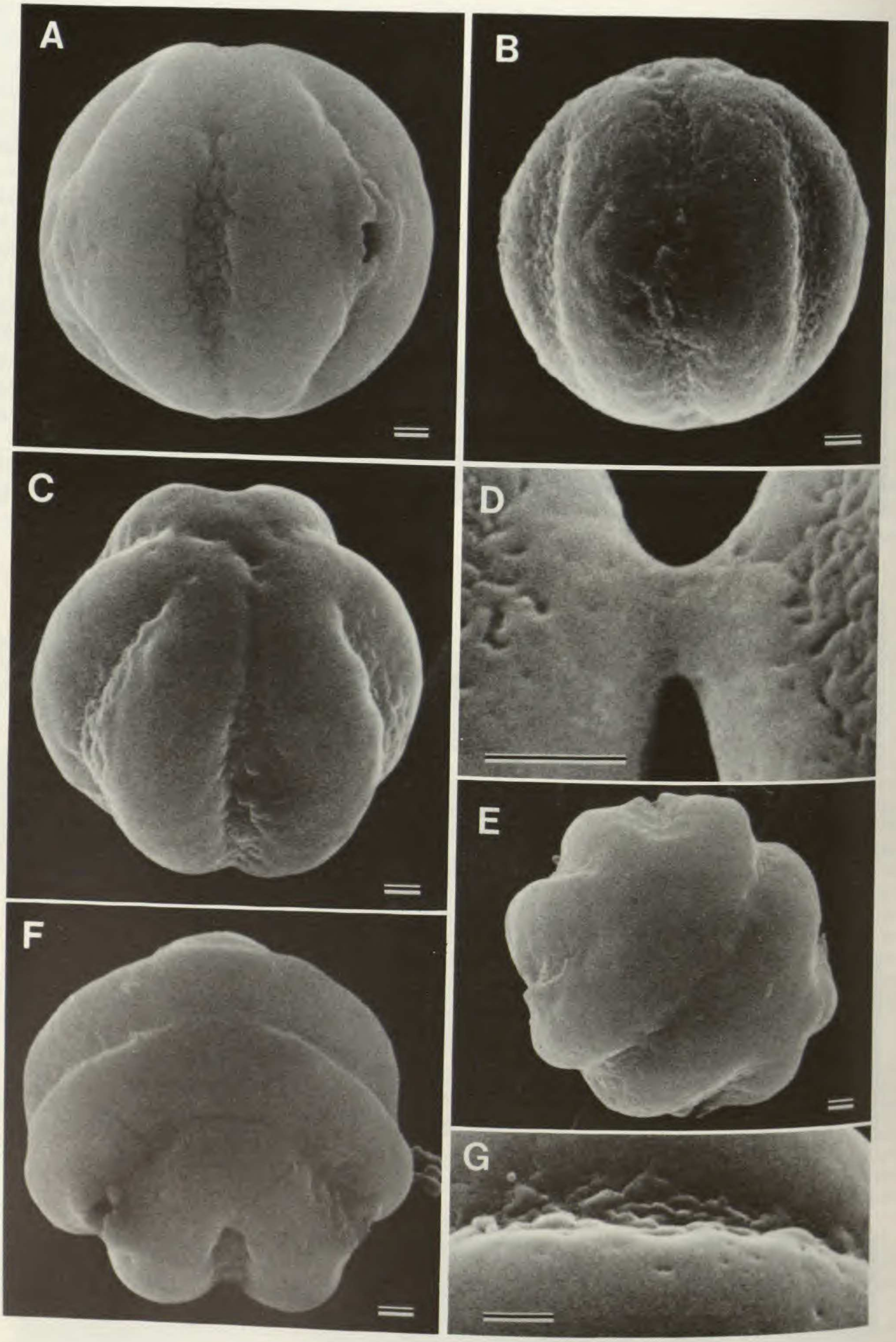
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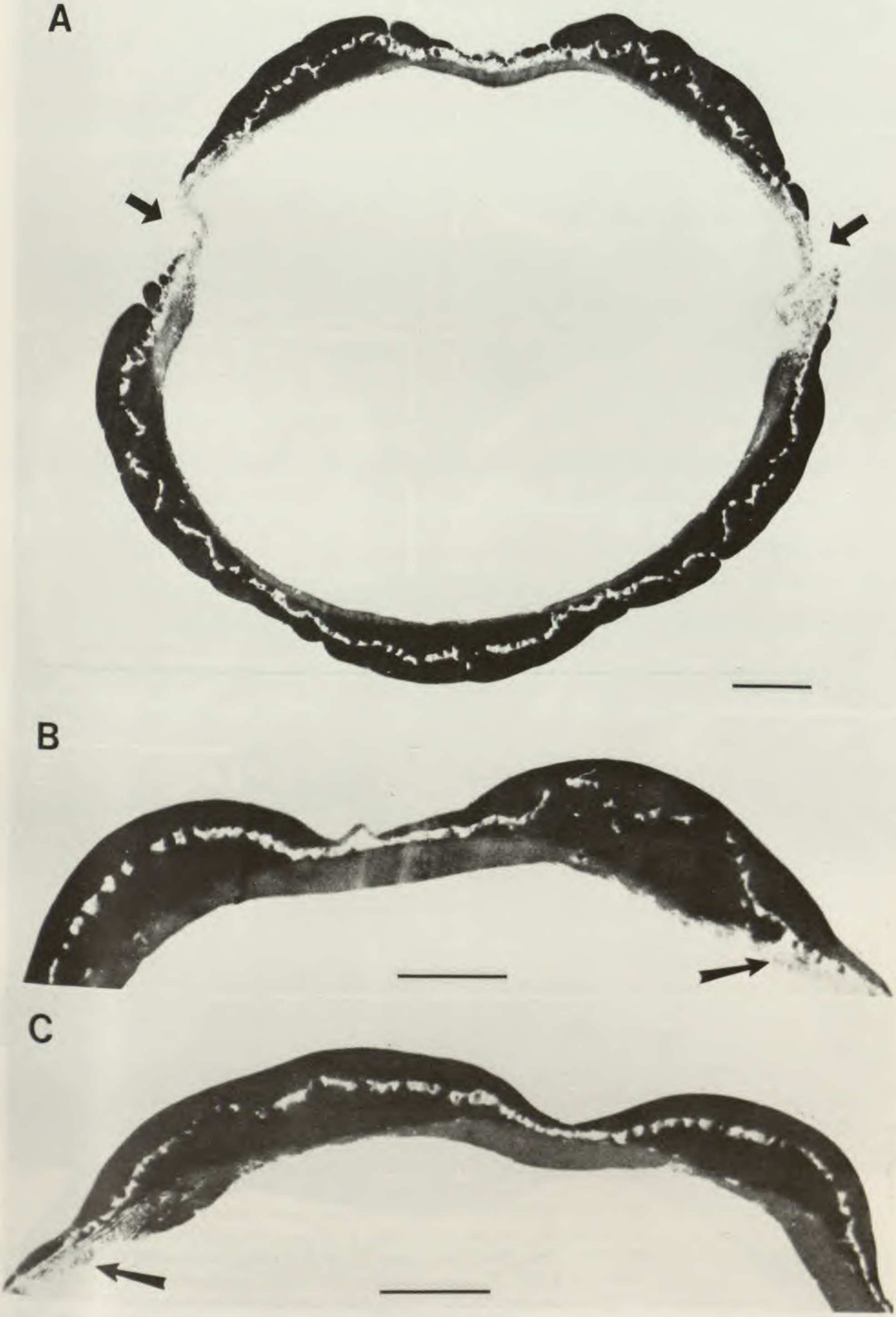
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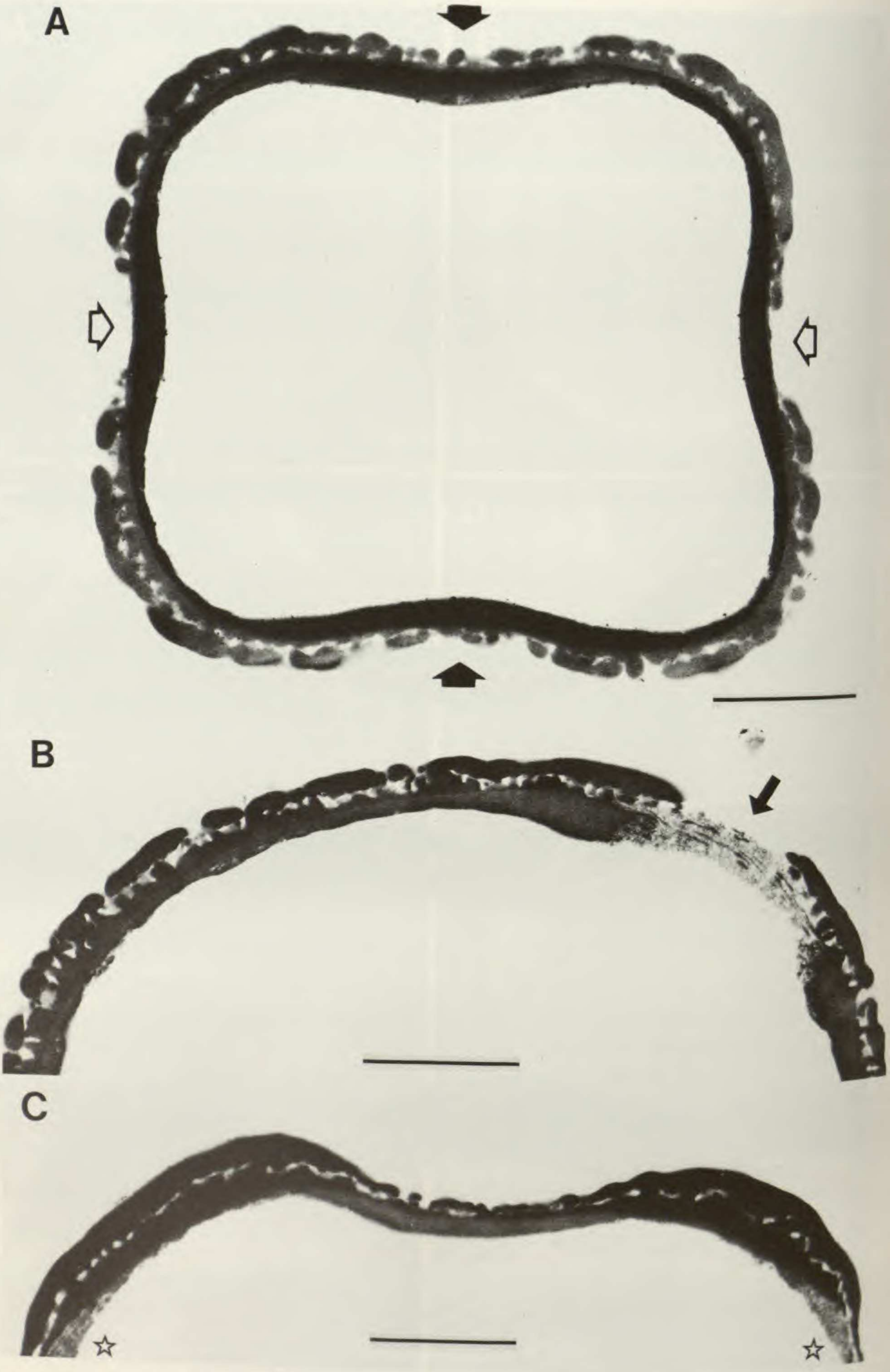


FIGURE 30. Transmission electron micrographs of Crypteroniaceae. — A. *Crypteronia leptostachys.* A vertical section of an entire grain passing through two colpi (open arrows) (which are syncolpi, and hence pass through the poles) and two subsidiary colpi (solid arrows). — B. *Crypteronia paniculata.* Section of a mesocolpium and an endoaperture (arrow). — C. *Axinandra zeylanica* (*Gunatilleke & Gunatilleke 582*). Section of two mesocolpia and the subsidiary colpus between them. The right mesocolpium shows a zig-zag columellae layer. Stars indicate endoapertures. Scales equal 1 μm.

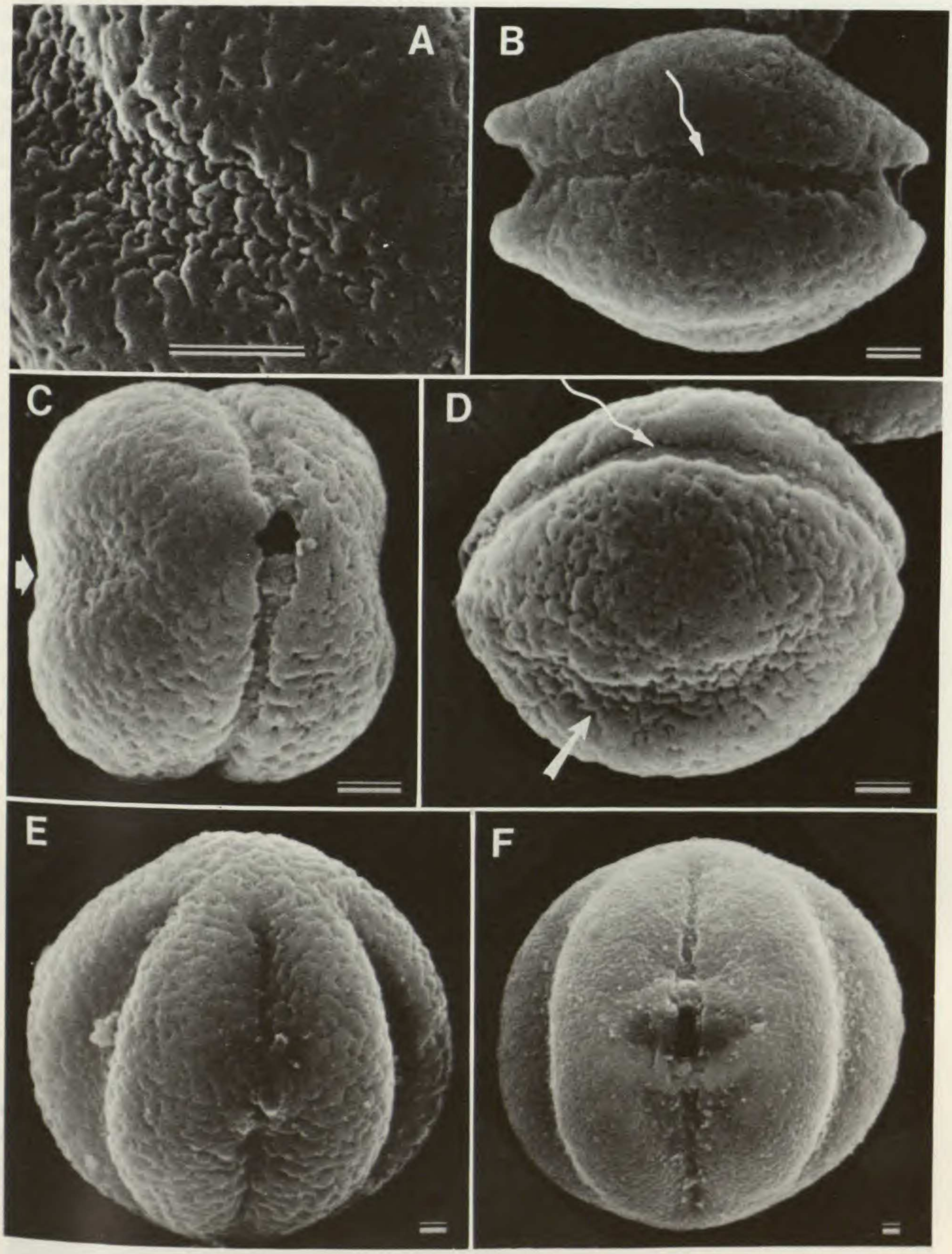
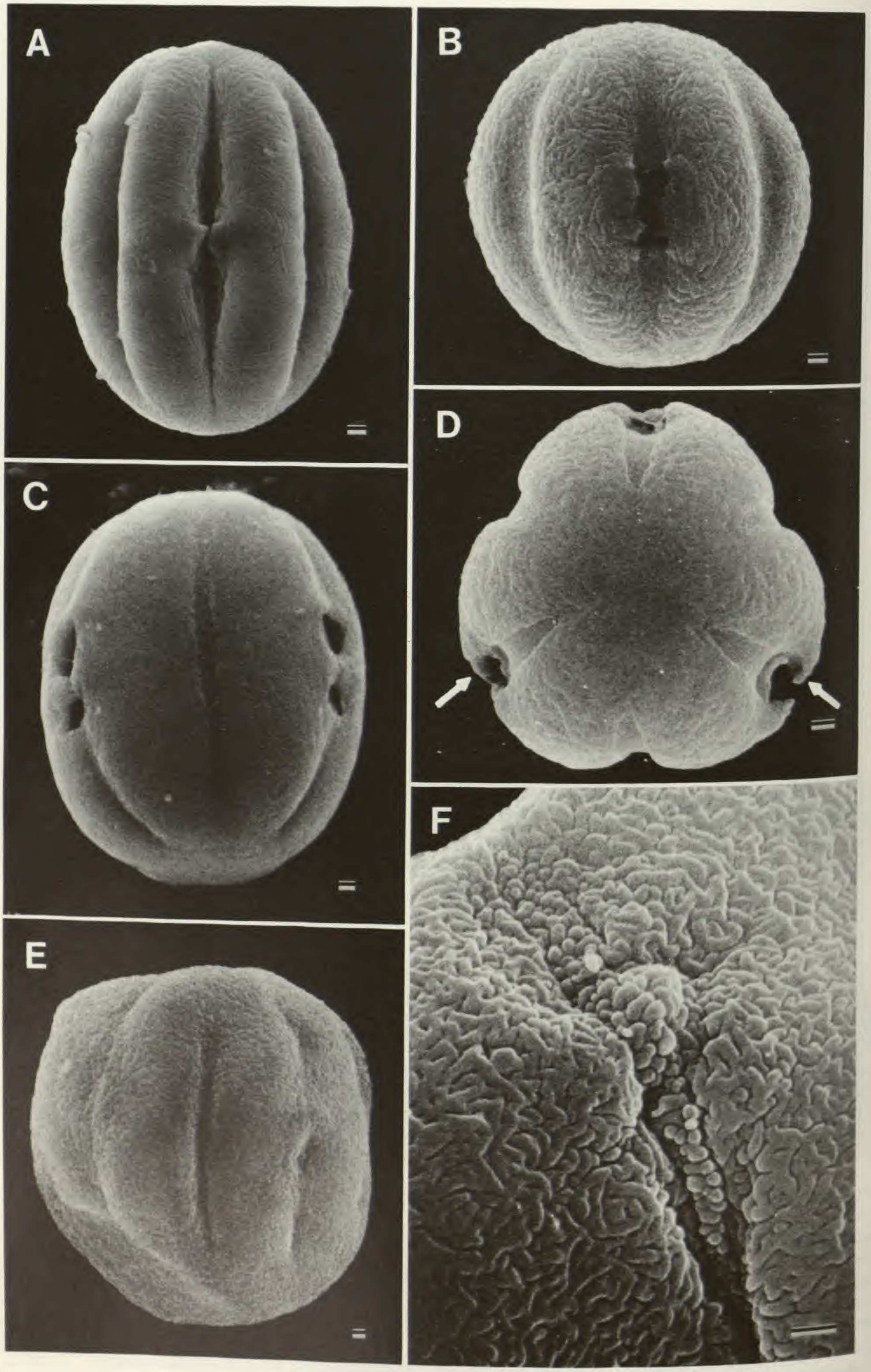


FIGURE 31. Scanning electron micrographs of pollen from Crypteroniaceae (A–D) and Melastomataceae (E, F).—A. *Crypteronia* sp. Enlarged portion of a subsidiary colpus and surrounding mesocolpia. The surface of the subsidiary colpus is granular-rugulate. B–D. *Crypteronia paniculata.*—B. Polar view. Arrow points to the pole over which passes the syncolpus. The two endoapertures (at the sides) are open.—C. Lateral view facing an endoaperture. Arrow indicates the laterally elongated intercolpar concavity.—D. Sublateral-subpolar view. The two colpi are united forming a circle passing through poles (wiggly arrow). Thick arrow indicates an intercolpar concavity.—E. *Memecylon normandii.* Sublateral view. The surface is rugulate.—F. *Mouriri glazioviana.* Lateral view. Note the elliptic, lalongate, thick-margined endoaperture. The surface consists of fine, elongate, branched muri. Scales equal 1 μm.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hondurensis, Fig. 35E), Combretaceae, Penaeaceae, Oliniaceae, and Lythraceae (*Lythrum, Peplis,* some species of *Ammannia, Nesaea,* and *Rotala*). Further, the *Crypteronia*-type pollen of Muller relates to Corynocarpaceae, Cunoniaceae, Eucryphiaceae, and Saxifragaceae (Muller, 1975; see also Erdtman, 1971). In endomorphology, *Dactylocladus* resembles *Alzatea,* Chrysobalanaceae (Patel et al., 1983a), and Corynocarpaceae (Nowicke & Skvarla, 1983) in having the zig-zag columellae layer.

MELASTOMATACEAE

Pollen of Melastomataceae is tricolporate, radially symmetrical, and isopolar. Grains are spheroidal to subprolate in lateral view with a circular, hexagonal, or triangular shape in the polar view. Monads are found in all taxa examined with the exception of *Tococa spadiciflora* which has polyads (Fig. 35F, H), and *Miconia melanotricha* (Fig. 35A, B) which has tetrads (Patel et al., unpubl. data). On the basis of exomorphology, three pollen groups can be established: heterocolpate with subsidiary colpi, "heterocolpate" with intercolpar concavities, and tricolporate.

In the heterocolpate group with subsidiary colpi, the three colpi (four in *Votomita*) alternate with three (four in *Votomita*) elongate, narrow subsidiary colpi. This type of pollen is present in *Trembleya phlogiformis* (Fig. 32A), *Tibouchina urvilleana* (Fig. 32C), *Tristemma littorale* (Fig. 32D), *Dissotis brazzae* (Fig. 33C, D), *Marumia nervosa* (Fig. 33A, B), *Dissochaeta celebica* (Fig. 33F), *Osbeckia polycephala* (Fig. 32B), *Acanthella sprucei* (Fig. 33E), *Memecylon normandii* (Fig. 31E), *Mouriri glazioviana* (Fig. 31F), *Votomita monadelpha* (Fig. 32E, F), *Miconia hondurensis* (Fig. 35D), *M. alypifolia* (Fig. 36A), *M. caesia* (Fig. 36D), *Comolia stenodon* (Fig. 36H), and *Tococa broadwayi* (Fig. 36F). The surface sculpture is variable. A more or less smooth surface with a few pits and punctae is present in *Acanthella* (Fig. 33E). In *Dissotis* (Fig. 33C, D) many channels, pits, and punctae are present on a smooth to rugulate surface. In *Marumia* (Fig. 33A, B), *Dissochaeta* (Fig. 33F), and *Memecylon* the surface is coarsely rugulate-punctate. It is striate-rugulate in *Tristemma* (Fig. 32D), *Comolia* (Fig. 36H), and *Osbeckia* (Fig. 32B), with elongate, more or less parallel muri, which in the latter become shorter and separated at the poles where the surface then becomes verrucate-rugulate. In *Trembleya* (Fig. 32A) and *Miconia alypifolia* (Fig. 36A) it is striate. In the latter species, bundles of striae are separated by large channels at the poles (Fig. 36A–C). In *Tibouchina* (Fig. 32C), it is smooth-punctate with a very faint striate pattern which in some grains is quite prominent at the poles. The finely rugulate surface in *Mouriri* (Fig. 31F) and *Votomita* (Fig. 32E, F) is composed of fine, elongate, branched, often overlapping muri that form a compact mesh with punctae. In *Miconia hondurensis* it is smooth-punctate (Fig. 35D, E). The surface of *M. caesia* (Fig. 36D) is distinctive in possessing a mesh of short, branched, cylindrical elements. In *Tococa broadwayi* (Fig. 36F), it is perforate.

Colpi are long (some grains are syncolpate in *Dissotis, Acanthella,* and *Dissochaeta*), with acute ends, and a smooth surface except in *Acanthella, Marumia,* and *Dissochaeta* where the surface is granular. In *Votomita,* the colpus surface is covered with bead-like elements. Endoapertures are lalongate (not clearly defined in *Dissochaeta*) and elliptic (circular to elliptic in *Votomita*). Extensions of the mesocolpia over the endoapertures are present (Figs. 32A, D, 33E, 36A). A horizontal bar is often persistent over the open endoapertures (Figs. 32C, 33A, D). Subsidiary colpi are long except in *Tococa broadwayi* (Fig. 36F), narrow, and have either a smooth, scabrate, or granular surface (Fig. 33B). They are usually

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FIGURE 32. Scanning electron micrographs of Melastomataceae pollen.—A. *Trembleya phlogiformis.* Lateral view showing extensions of the mesocolpia over the endoaperture (at center) and two subsidiary colpi. The exine surface is striate.—B. *Osbeckia polycephala.* Lateral view. The exine surface is rugulate.—C. *Tibouchina urvilleana.* Sublateral view with a subsidiary colpus at center. A horizontal ektexinous bar appears to divide the endoapertures into two parts (see legend discussion to *Sonderothamnus petraeus,* Fig. 19F).—D. *Tristemma littorale.* Polar view. Extensions of mesocolpia are apparent over the endoapertures (arrows). E, F. *Votomita monadelpha.*—E. Lateral view with a subsidiary colpus at center. Although not evident in this figure there are four colpi alternating with four subsidiary colpi.—F. The fine, elongate, branched surface units of the mesocolpia contrast with bead-like units of the colpus. This surface is somewhat similar to the pollen of *Boisduvalia* (Onagraceae, Fig. 52B, C, E) although it does not appear to be perforate. Scales equal 1 μm.

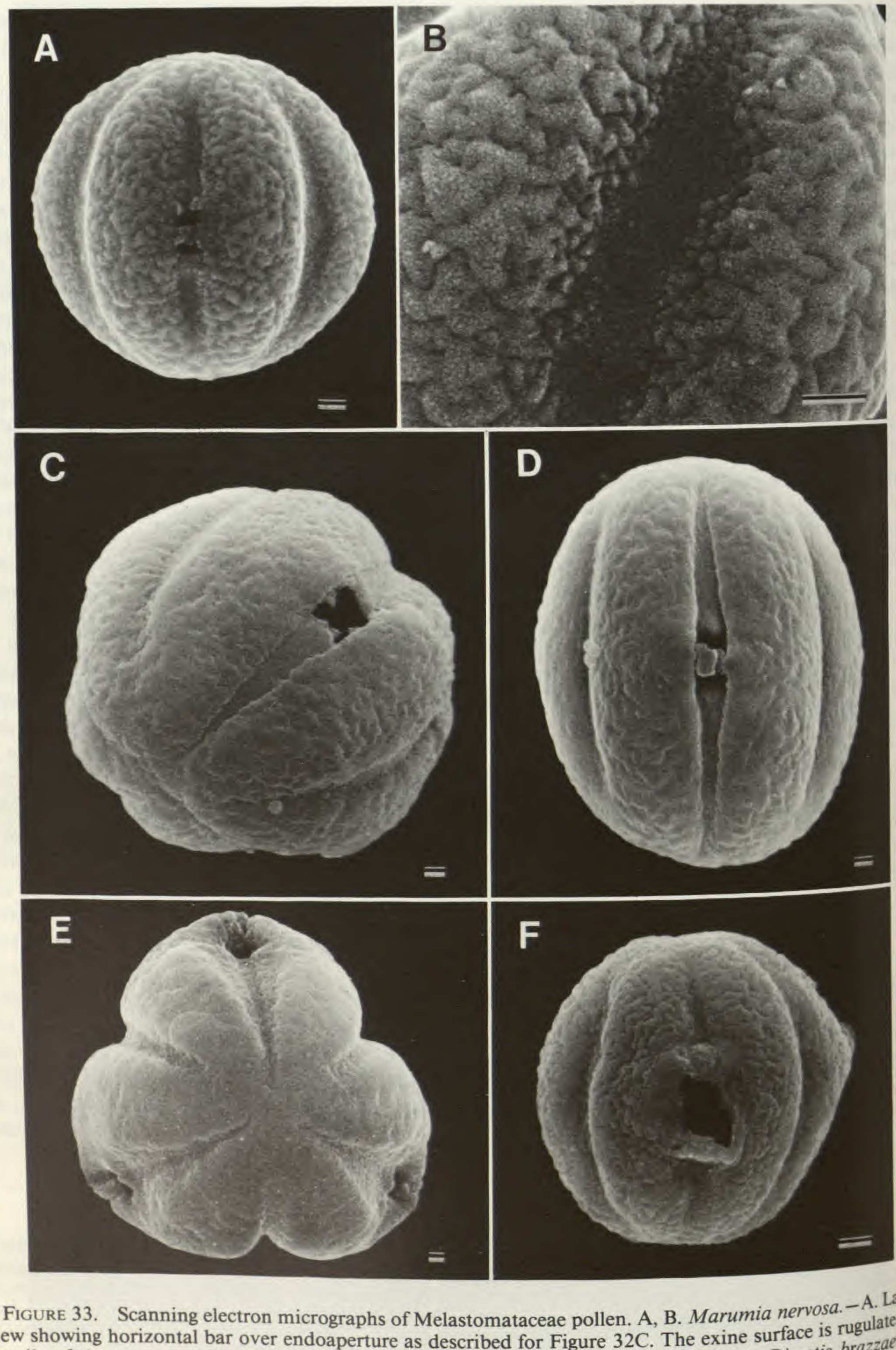

FIGURE 33. Scanning electron micrographs of Melastomataceae pollen. A, B. *Marumia nervosa*.—A. Lateral view showing horizontal bar over endoaperture as described for Figure 32C. The exine surface is rugulate.—B. Details of the granular subsidiary colpus and surrounding rugulate mesocolpia. C, D. *Dissotis brazzae*.—C. Subpolar view. The colpi are united at the pole. The surface is rugulate.—D. Lateral view. See discussion to Figure 32C concerning horizontal bar over endoaperture.—E. *Acanthella sprucei*. Polar view. The surface is smooth with a few channels and pits. Extensions of the mesocolpia over the endoapertures are prominent.—F. *Dissochaeta celebica*. Lateral view. The surface is rugulate. Scales equal 1 μm.

shorter than the colpi but in *Marumia* and *Dissochaeta* they are as long as or longer than the colpi. Some grains of *Miconia hondurensis* (Fig. 35E) are bilateral, dicolporate, syncolpate with two large intercolpar concavities. In addition to the usual tricolporate-isopolar pollen of *M. alypifolia* there are present: (1) grains with various arrangements of colpi and subsidiary colpi (Fig. 36C), (2) heteropolar grains (Fig. 36C), and (3) grains with both subsidiary colpi and intercolpar concavities (occurring in pollen with more than three colpi, Fig. 36B).

In the second group, "heterocolpate" with intercolpar concavities, there are present on the mesocolpia three intercolpar concavities—large, elliptic, thin-walled, depressed areas. The remaining thick-walled portion of the mesocolpia forms a more or less narrow band around the intercolpar concavities. This type of pollen is illustrated by *Adelobotrys tessmannii* (Fig. 34A–C), *Allomorphia caudata* (Fig. 34D), *Bredia hirsuta* (Fig. 34F), *Astronia cumingiana* (Fig. 34E), *Oxyspora paniculata* (Fig. 34G, H), and *Miconia melanotricha* (Fig. 35A–C). The grains are spheroidal in lateral view and circular to triangular or hexagonal (*Oxyspora*) in polar view. Colpi are long and narrow with acute ends and a more or less smooth surface. Extensions of the mesocolpia are present over the lalongate, elliptic endoapertures (Figs. 34D, E, 35A, B, D, not clearly defined in *Allomorphia,* not examined in *Astronia*). *Adelobotrys* differs from the other taxa in having wide colpi that are united at the poles, and by a granular-verrucate surface. The colpus membrane is raised over the endoaperture (Fig. 34B, arrow). This raised membrane is vertically oriented and does not seem to be analogous with an operculum.

The surface of the meso- and apocolpia is variable: psilate in *Adelobotrys* (Fig. 34A–C), scabrate in *Allomorphia* (Fig. 34D, although not very clear), striate-rugulate in *Oxyspora* (Fig. 34G, H), fine rugulate-verrucate in *Bredia* (Fig. 34F), smooth-punctate in *Miconia* (Fig. 35C), and coarse with many channels and pits (rugulate ?) in *Astronia* (Fig. 34E). The intercolpar concavities differ in size and surface sculpture. In *Bredia* and *Astronia,* the surface sculpture of the concavities is similar to that of the rest of the grain except that it is finer. *Adelobotrys* and *Allomorphia* have a verrucate surface while *Oxyspora* has angular, flat, irregularly shaped units on the surface of the intercolpar concavities. In *Miconia* the surface is granular-verrucate.

Exine structure is similar in both pollen groups described above. In the meso- and apocolpia the foot layer is well developed and often dome-shaped (Figs. 37B, D, 38A, 39A). Here the endexine is less developed and often very thin (Fig. 38A, B). A "white line" between the foot layer and the endexine is often distinct (Figs. 37B, C, 38A). The columellae are short, erect, and distally branched. The tectum is thick, perforate, and has an undulating outer margin, although in *Adelobotrys* (Fig. 39A) perforations are rare and the outer margin of the tectum is smooth. *Acanthella* (Fig. 38D) differs from the other taxa in having a very thick tectum (rarely perforate) and thick foot layer that are separated by columellae that appear granular and have lateral extensions.

Toward the colpi and subsidiary colpi or the intercolpar concavities, the endexine becomes thicker whereas the ektexine layers taper. The foot layer is discontinuous and thinner at the margins of the mesocolpia: on the surface of the colpi, subsidiary colpi, and intercolpar concavities, it remains either as a very thin layer (Figs. 38A, 39A, B, D) or is absent. The tectum is thin, the columellae are short and fine, or they are both absent. In the intercolpar concavities, the verrucae (or the irregular elements in *Oxyspora*) show a thin, dome-shaped tectum below which one or more fine columellae are present (Fig. 39A, B, D). In *Astronia* the tectum is thin and columellae are irregular and short (Fig. 39C).

In the region of the endoaperture, the endexine is thick and granular and often lamellate (e.g., *Adelobotrys, Trembleya*). The tectum is thinner and the columellae are shorter. The foot layer is tapered leaving the columellae and tectum directly overlying the granular endexine (Figs. 38D, 39A, C, D). Around the endoaperture in *Astronia* (Fig. 39C) the columellae and tectum are separated from the endexine.

The third, tricolporate group, is represented by *Tococa stephanotricha* (Fig. 36E) and *T. formicaria* (Fig. 36G), which have a rugulate surface and very short colpi. In TEM of *T. stephanotricha* (Fig. 40B, C) the endexine is uniform in thickness except near the endoapertures where it is thicker, granular, and lamellate. The foot layer is also uniform in thickness. The columellae are short, erect or reclining, and rarely branched. The tectum is discontinuous with irregular dome-like units in section.

A third species of *Tococa, T. spadiciflora,* could not be assigned to any of the three groups described above. It consists of polyads which are composed of basic units of tetrahedral tetrads (Fig. 35F–I). Internal bridges on the proximal faces of individual pollen grains maintain tetrad unity while external bridges on the distal faces of the tetrads, frequently along the aperture margins, maintain polyad unity (Fig. 35G–I). Individual grains are usually tetracolporate but grains with five or more colpi have also been noted. Colpi are long with acute ends and have a smooth surface. Some grains appear to have colpi of unequal length. Endoapertures are lalongate and elliptic. The meso- and apocolpia surface is smooth-punctate. Subsidiary colpi are difficult to characterize and are either weakly developed or absent. In TEM (Fig. 40A), the endexine is more or less uniform in thickness except near the endoapertures where it is thicker and granular. The foot layer is uniform in some areas but in others it is highly irregular and discontinuous with many channels and gaps. Columellae are long, thick, and erect, and they split at their distal ends into fine, very short branches. The tectum is thick and uniform, with large perforations. The tectum as well as the columellae show fusion at the points of attachment between members of the polyads.

Discussion

As indicated earlier, Melastomataceae pollen has received little study above the light microscope level. Guers (1974) included scanning electron micrographs of *Dicellandra barteri, Calvoa orientalis,* and *Osbeckia decandra.* These were part of a light microscope study of eight genera and 20 species from tropical Africa. *Dicellandra* and *Calvoa* compare favorably with our second pollen group in possessing intercolpar concavities; in contrast, *O. decandra* compares with our first pollen group.

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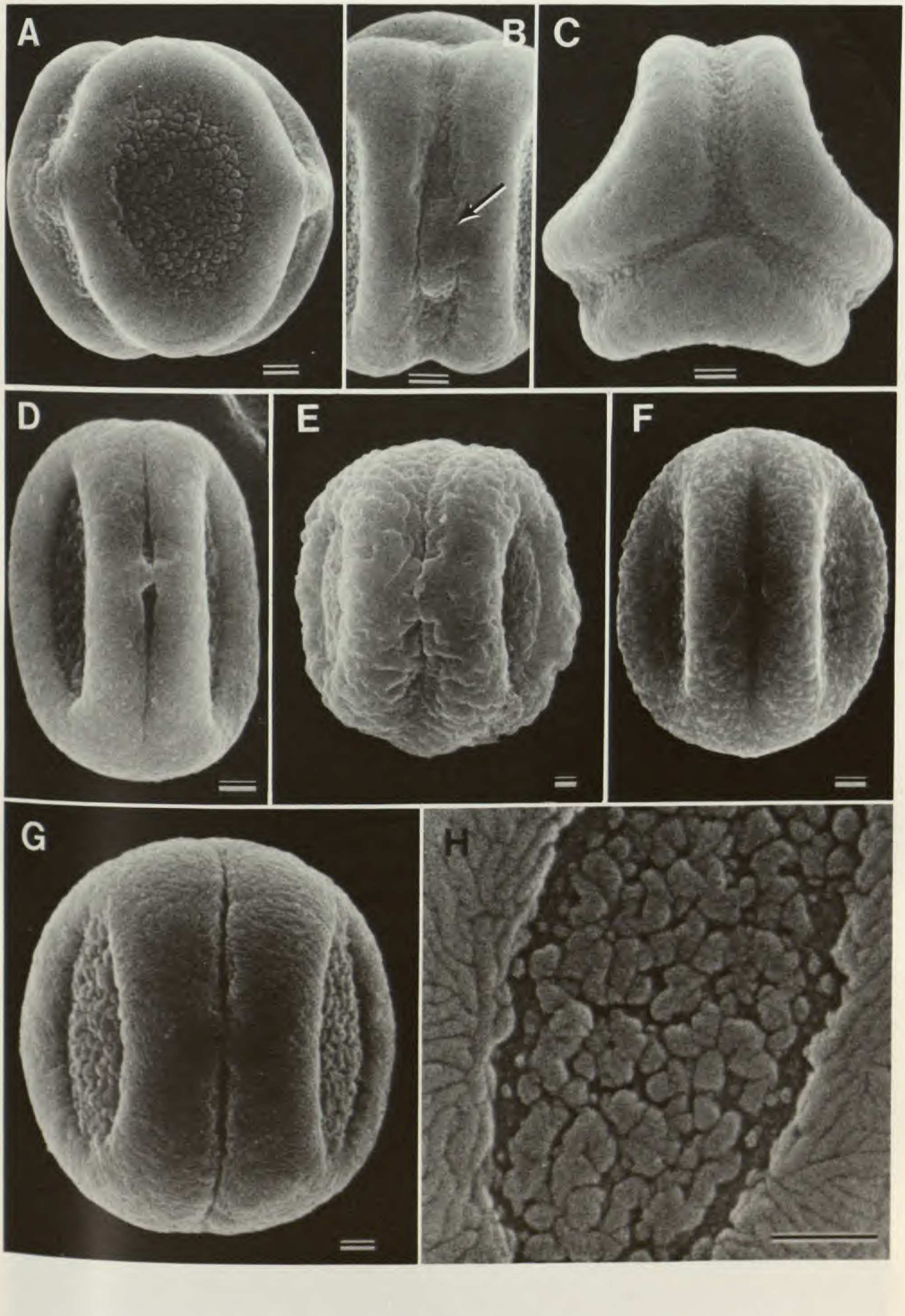
FIGURE 34. Scanning electron micrographs of Melastomataceae pollen. A–C. *Adelobotrys tessmannii.*—A. Lateral view showing an intercolpar concavity with a verrucate surface. The surrounding mesocolpia are narrow and have a psilate surface. The colpi are united at the poles (i.e., syncolpate).—B. Lateral view showing a colpus. The colpus membrane is raised over the endoaperture (arrow).—C. Polar view showing united colpi with a granular surface. The concave sides of the pollen grain are due to the thin-walled intercolpar concavities. In a wet grain they bulge, giving it a circular shape.—D. *Allomorphia caudata.* Lateral view. The colpus is narrow and wide extensions of the mesocolpia are present over the endoaperture. The intercolpar concavities have a verrucate surface. Elsewhere the surface is smooth.—E. *Astronia cumingiana.* Lateral view. The surface is coarsely rugulate. The colpus is very narrow. Note the large mesocolpial extensions (see Fig. 39C). The surface of the intercolpar concavities is also rugulate but not as coarse as the rest of the grain.—F. *Bredia hirsuta.* Lateral view. The surface is rugulate. The intercolpar concavities are also rugulate but with a finer surface. G, H. *Oxyspora paniculata.*—G. Lateral view. The surface is striate. The colpus is very narrow and long.—H. Enlarged view of the intercolpar concavity and the surrounding area. Irregular, flattened elements are present on the surface of the concavity. Scales equal 1 μm.

FIGURE 35. Scanning electron micrographs of Melastomataceae pollen. A–C. *Miconia melanotricha.*—A. A tetrahedral tetrad. Exine bridges connect tetrad members.—B. Three grains of a tetrad. The fourth grain is missing as indicated by broken bridges (arrow).—C. The bridges are narrow and have a smooth surface. The surface of the mesocolpia is smooth-punctate, that of the intercolpar concavities is granular-verrucate. D, E. *Miconia hondurensis.*—D. Polar view of a tricolporate grain. Three subsidiary colpi alternate with the colpi.—E. Sublateral view of a bilateral, dicolporate, syncolpate grain with two intercolpar concavities. Here the visible intercolpar concavity (large arrow) is meridionally elongated. In some dicolporate, syncolpate grains, it is laterally elongated similar to *Crypteronia* (Fig. 31B–D) pollen. The syncolpus circles the grain vertically. Small arrow indicates the position of an endoaperture. F–H. *Tococa spadiciflora* (*Archer 1976*).—F. A polyad.—G. A grain from a polyad showing bases of broken exine bridges on the margins of a colpus. The colpus at the center (arrowhead) appears to be shorter than the one on the right, and also at a slight angle to the polar axis. Two lines (top arrows) above the short colpus form a triradiate configuration. This phenomenon was observed in other grains, but pollen with meridionally arranged colpi appear to be more common.—H. An octad.—I. *T. spadiciflora* (*Forero et al. 5703*). An exine bridge between two grains. It is thick and has a punctate surface similar to that of the grains. Some punctae contain granules. Unless otherwise indicated, scales equal 1 μm.

FIGURE 36. Scanning electron micrographs of Melastomataceae pollen. A–C. *Miconia alypifolia.*—A. Lateral view. Note the striate-punctate surface near the equator. Toward the poles the surface becomes coarse.—B. Polar view of a six-colporate grain with subsidiary colpi (arrow) and intercolpar concavities (arrowhead). Such grains are rare.—C. Subpolar view of a heteropolar, conoidal (Muller, 1978b) grain. The two visible colpi (arrows) are united.—D. *M. caesia.* Polar view.—E. *Tococa stephanotricha.* Polar view.—F. *T. broadwayi.* Sublateral view. Subsidiary colpi are not as well developed as in other taxa of the family.—G. *T. formicaria.* Lateral view.—H. *Comolia stenodon.* Subpolar view. Scales equal 1 μm.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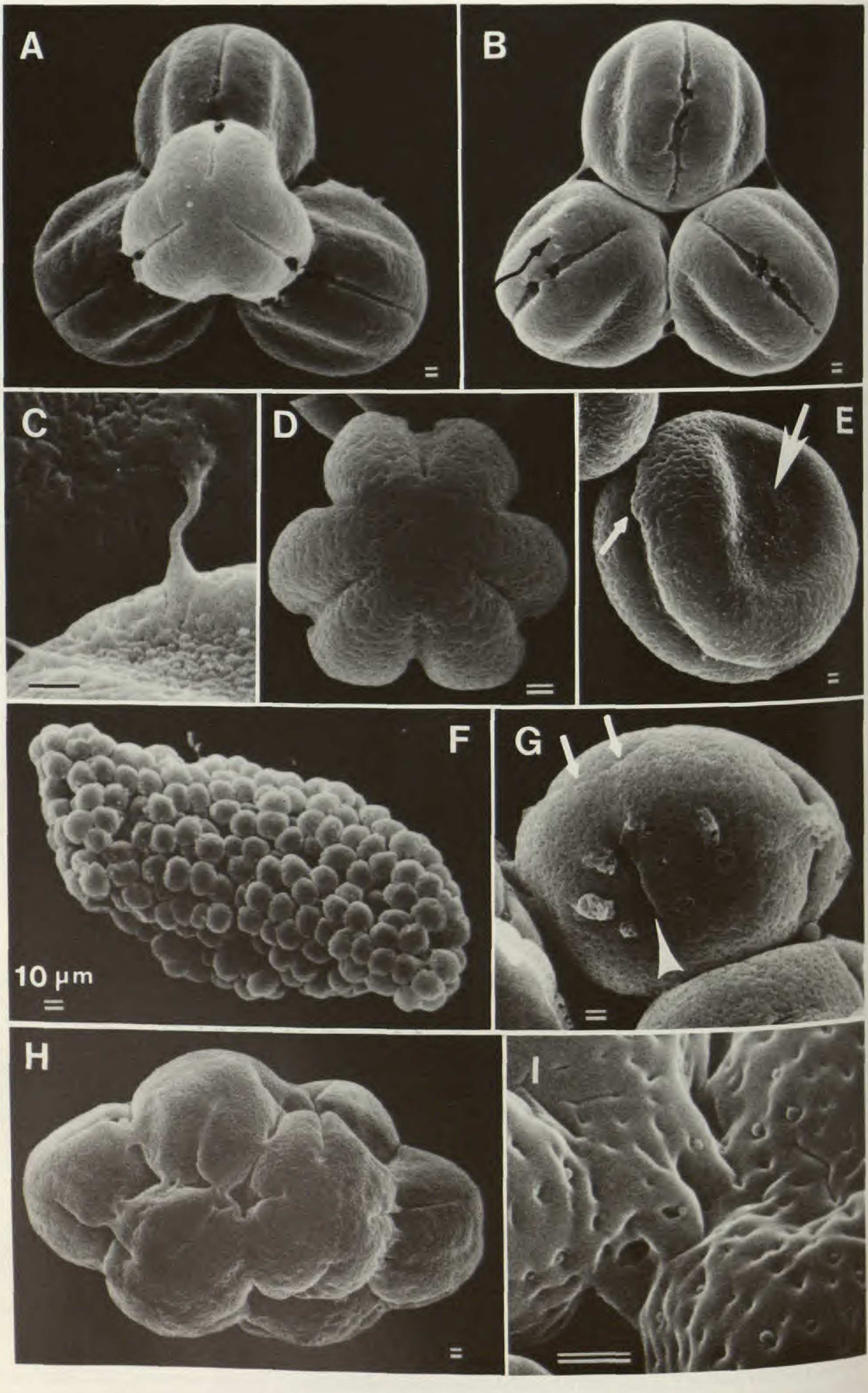
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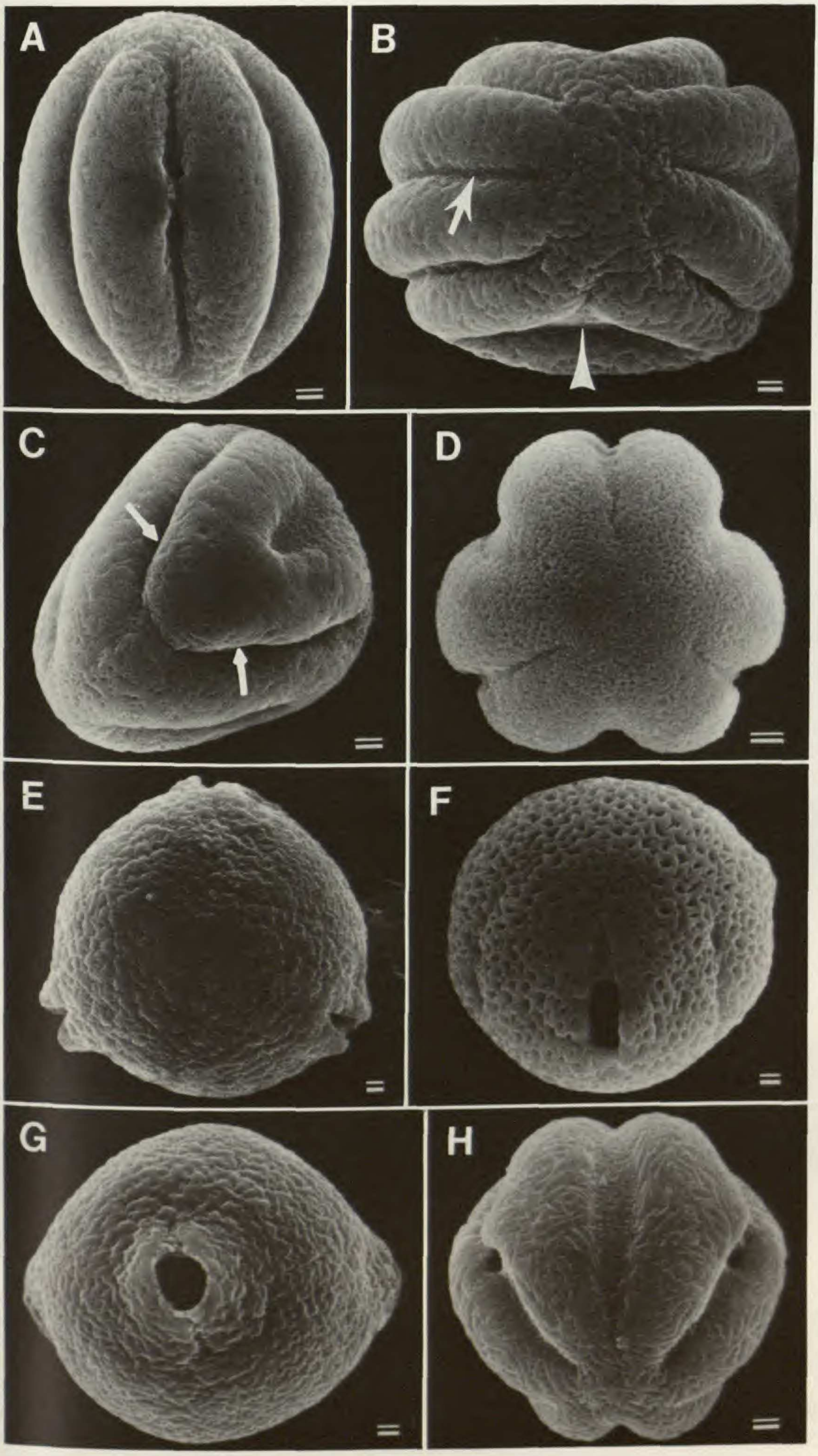
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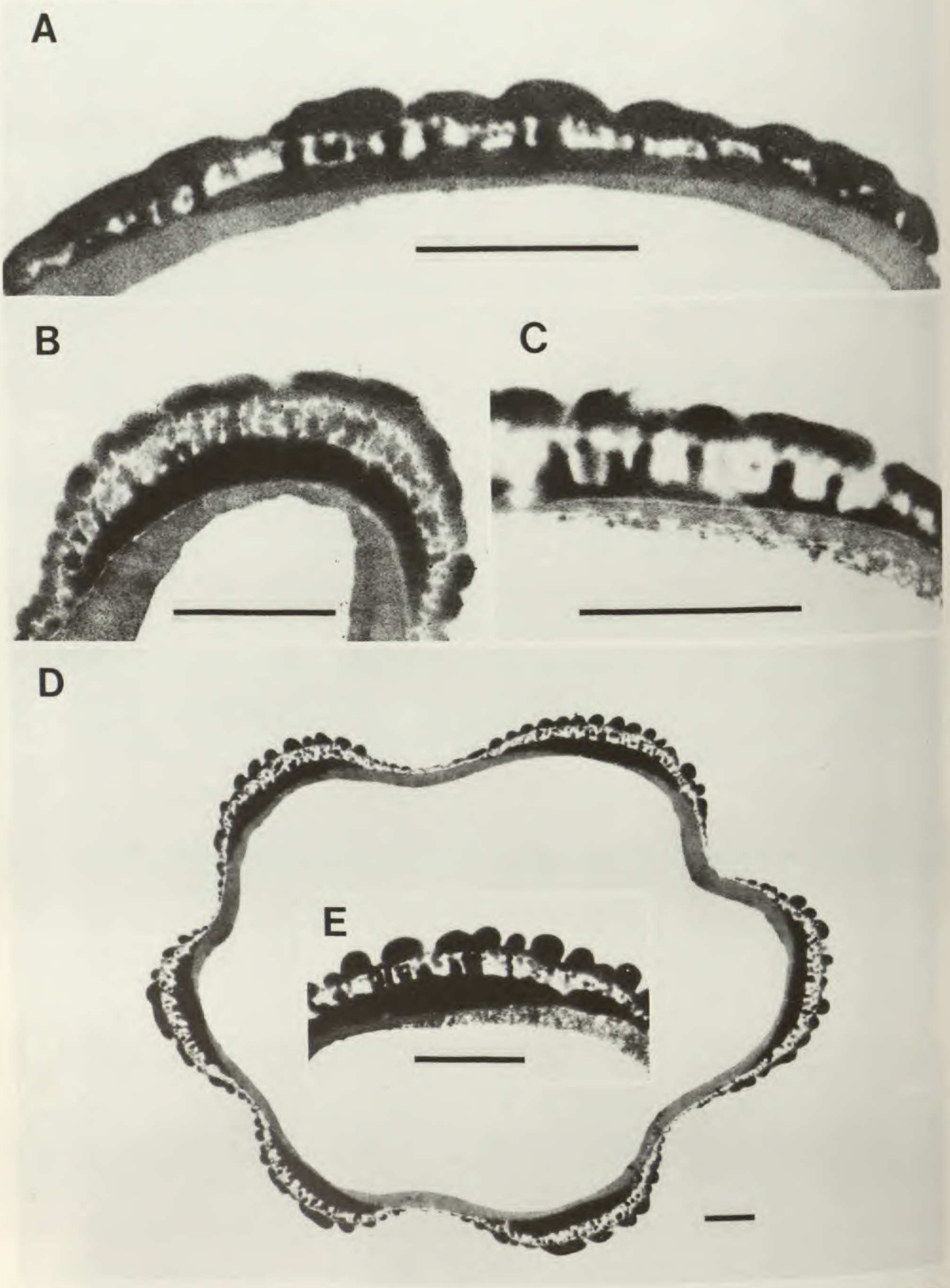


FIGURE 37. Transmission electron micrographs of Melastomataceae pollen. — A. *Tristemma littorale.* Section of a mesocolpium. — B. *Trembleya phlogiformis.* An oblique section of a mesocolpium which is folded due to the collapsed grain. The columellae are numerous and markedly branched. — C. *Tibouchina candolleana.* A portion of the mesocolpium near an endoaperture (not included here). The endexine is granular-lamellate. D, E. *Osbeckia polycephala.* — D. Cross section of an entire grain. Because the section does not include the equator or endoapertures, colpi and subsidiary colpi cannot be identified. — E. Mesocolpium near an endoaperture. The tectum is deeply lobed due to striae. Scales equal 1 μm.

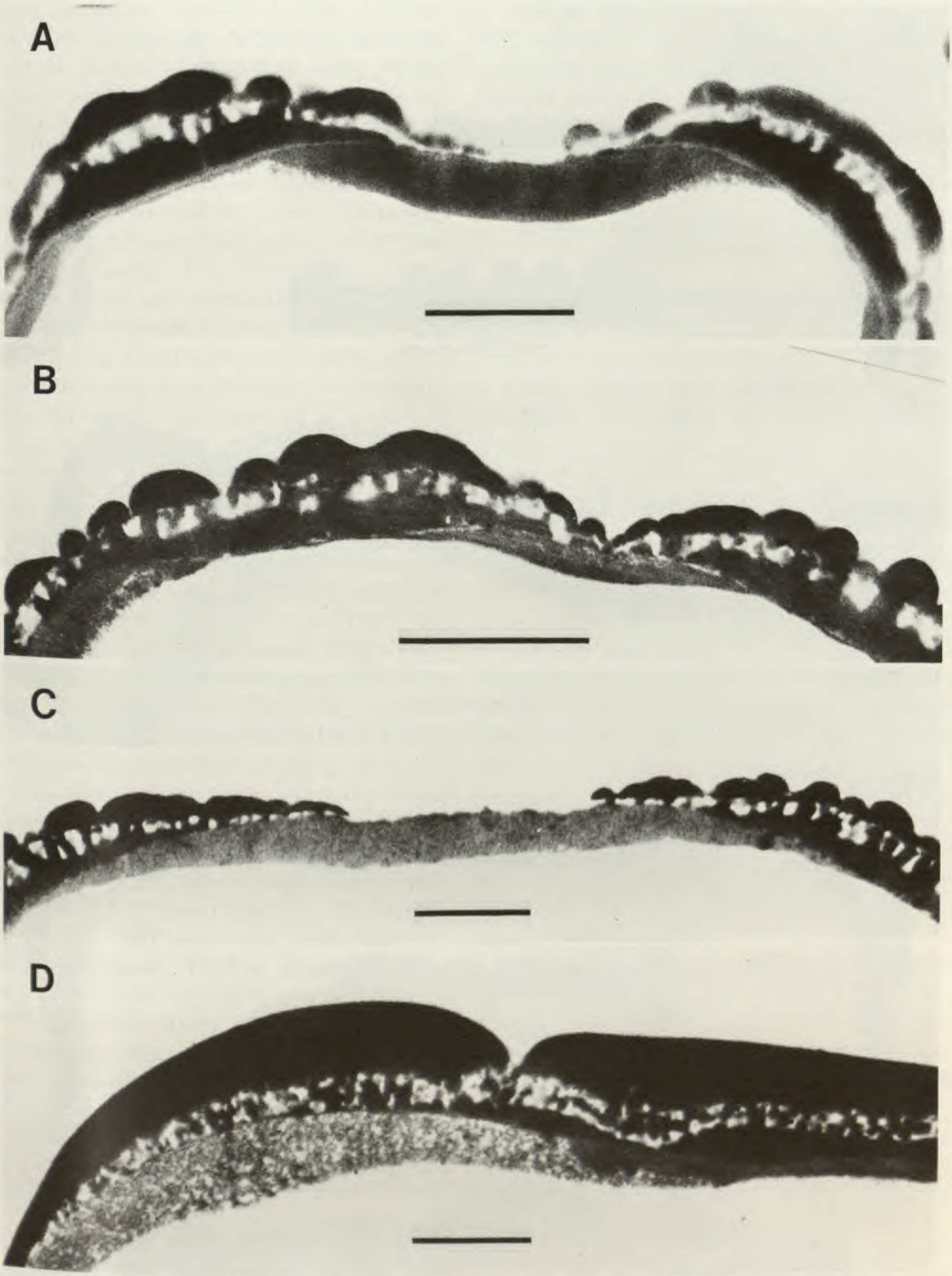
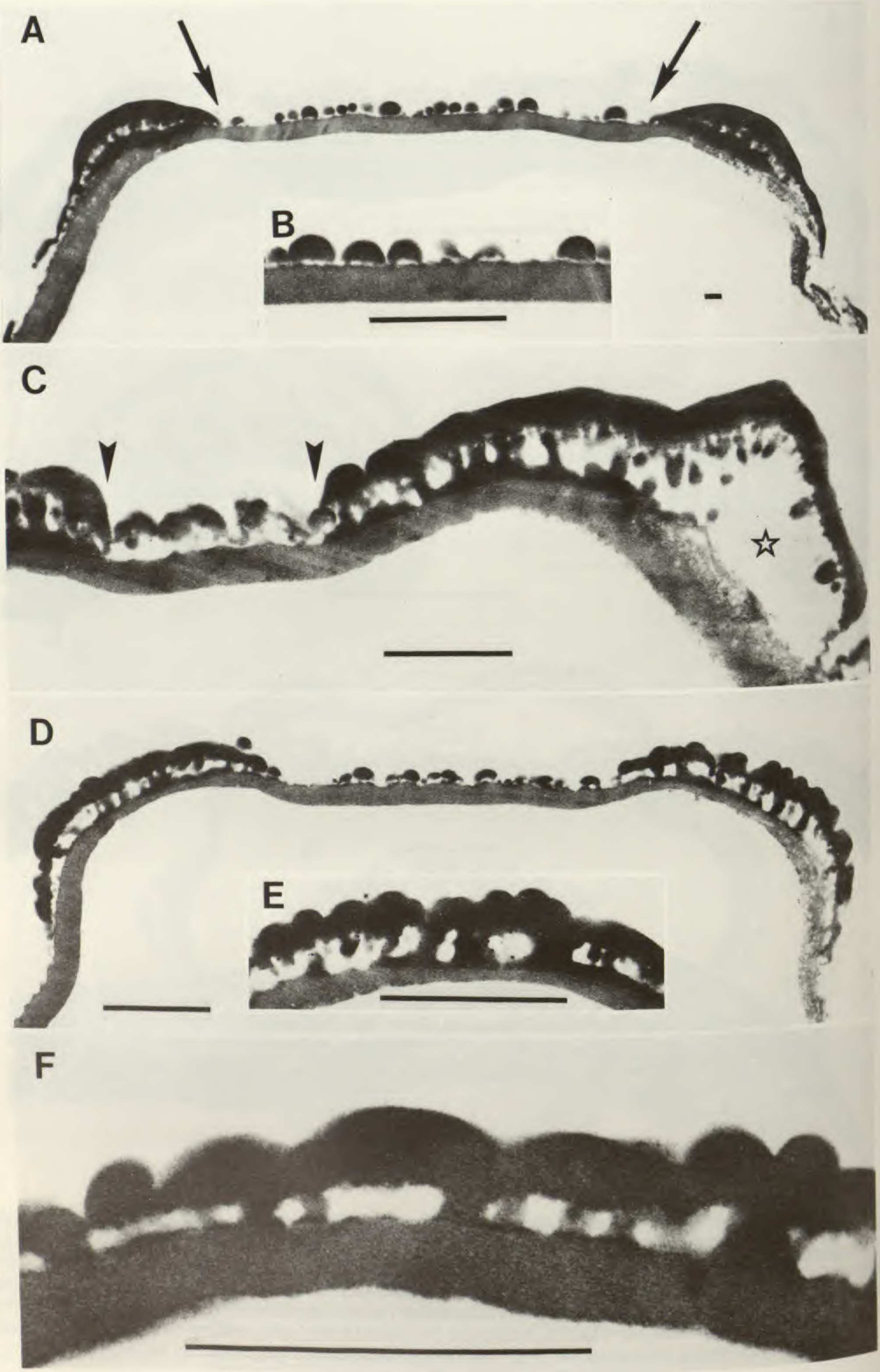


FIGURE 38. Transmission electron micrographs of Melastomataceae pollen.—A. *Marumia nervosa.* Section of two mesocolpia and a colpus or subsidiary colpus between them. The dome-shaped foot layer is similar to Combretaceae pollen (Fig. 20A, B, D, F).—B. *Dissochaeta celebica.* Similar to Figure 37A.—C. *Dissotis brazzae.* Similar to Figure 37A, B.—D. *Acanthella sprucei.* Mesocolpium in the region of an endoaperture. The tectum is very thick with rare perforations. The granular appearing columellae have lateral extensions. Toward the colpus the thick foot layer is reduced while the endexine increases in thickness and becomes granular. Note the general similarity to the pollen of Oliniaceae (Fig. 14B–E) and Penaeaceae (Fig. 26A, B, D). Scales equal 1 μm.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Among the genera examined here, *Mouriri, Votomita,* and *Memecylon* have often been segregated with several other genera from Melastomataceae sensu stricto as Memecylaceae or subfamily Memecyloideae (e.g., Dahlgren & Thorne, 1984; Johnson & Briggs, 1984). All three of these genera belong to the heterocolpate group, but they are not delimited as a group in any way from the other heterocolpate genera of Melastomataceae, although *Votomita* is unusual in having four colpi and subsidiary colpi, and a bead-like colpus surface. Further studies on this group, including *Lijndenia, Spathandra, Warnecka,* and more species of *Memecylon,* and particularly *Pternandra,* are essential to a proper understanding of the relationships between Melastomataceae sensu stricto and Memecyloideae.

Within the limited context of this study only those taxa in our first pollen type, that is, the heterocolpate type, show some similarities to other core families. At the SEM level some resemblance is evident with *Combretum* (Fig. 15A, B), *Bucida* (Fig. 17A), *Conocarpus* (Fig. 17B), *Pteleopsis* (Fig. 17C), *Terminalia* (Fig. 17D), *Ramatuella* (Fig. 17E), *Guiera* (Fig. 18E), *Poivrea* (Fig. 19C), and *Lumnitzera* (Fig. 19D) of Combretaceae; and *Sonderothamnus* (Fig. 25E) of Penaeaceae. Some of the bilateral, dicolporate, syncolpate grains in *Miconia hondurensis* (Patel et al., unpub. data) recall *Crypteronia.* At the TEM level the striking dome-shaped foot layer of the heterocolpate type (Figs. 37, 38, except *Acanthella* Fig. 38D) compares with that in Combretaceae (Fig. 20). TEM of *Acanthella* (Fig. 38D) is notably distinctive in Melastomataceae, resembling to some extent *Penaea* (Fig. 26A), *Sonderothamnus* (Fig. 26B, D), *Saltera* (Fig. 27D), and *Stylapterus* (Fig. 27E) of Penaeaceae; and *Olinia* (Fig. 14B–E) of Oliniaceae.

TEM of the other two pollen types (Figs. 39, 40) does not reveal any significant comparisons other than those already mentioned in the plate legends and pollen descriptions. Clearly, pollen in this family must be investigated in greater depth.

MYRTACEAE (INCLUDING PSILOXYLACEAE AND HETEROPYXIDACEAE)

In general, the pollen is tricolporate (triporate in *Tristania nereifolia*), radially symmetrical, and isopolar or heteropolar. In lateral view the pollen is oblate, elliptic with obtuse or truncate sides (Reitsma, 1970). In polar view it is triangular, goniotreme with straight or curved sides (convex or concave), and with acute or obtuse corners. Colpi vary in length, are either syncolpate or parasyncolpate, and generally have a smooth surface. Endoapertures are lalongate. Intercolpar concavities are present in some species. Heteropolar grains are due either to the nature of the colpi (e.g., long on one pole and syncolpate on the other pole), or to the different shapes (concave, convex, straight) of the two polar faces. In *Eugenia capuli,* and in some grains of *Luma chequen, Chamelaucium unciniatum, Temu divaricatum,* and *Ugni molinae,* one polar face is concave (or straight, in *Chamaelaucium*) and the other is convex. The pollen is free except in *Myrtus communis* (Fig. 48D) and *Psidium littorale* (Fig. 46B), where tetrahedral tetrads are present along with the monads.

Based on the nature of colpi, Pike (1956) recognized three pollen types in the Myrtaceae from the southwest Pacific area: (1) longicolpate grains; (2) syn- or parasyncolpate grains, and (3) brevi- or brevissimicolpate grains. All three types are present in the taxa examined in this study.

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FIGURE 39. Transmission electron micrographs of Melastomataceae pollen. A, B. *Adelobotrys tessmannii.*—A. Section including approximately one-third of an entire grain. Colpi and mesocolpia are on the sides of a large intercolpar concavity (between arrows). The mesocolpia consist of a thick imperforate tectum, short columellae, and a thick foot layer. In the intercolpar concavity, the verrucae of scanning electron micrograph (Fig. 34A) are dome-shaped and are supported by fine columellae and a thin foot layer. The endexine is thicker below the intercolpar concavity than below the mesocolpia.—B. Detail of a portion of the intercolpar concavity as described for A.—C. *Astronia cumingiana.* Section of a mesocolpium near a colpus (right) and an intercolpar concavity (between arrowheads). In the intercolpar concavity the tectum is folded or undulated while columellae and foot layer are not apparent in this plane of section. In the colpus region the area marked with a star is equivalent to the wide mesocolpial extensions noted in scanning electron micrograph (see Fig. 34E). D, E. *Oxyspora paniculata.*—D. Cross section of approximately one-third of an entire grain including two colpi (on the sides), two mesocolpia, and an intercolpar concavity.—E. Enlarged area of a mesocolpium.—F. *Bredia hirsuta.* Section of a mesocolpium. Scales equal 1 μm.

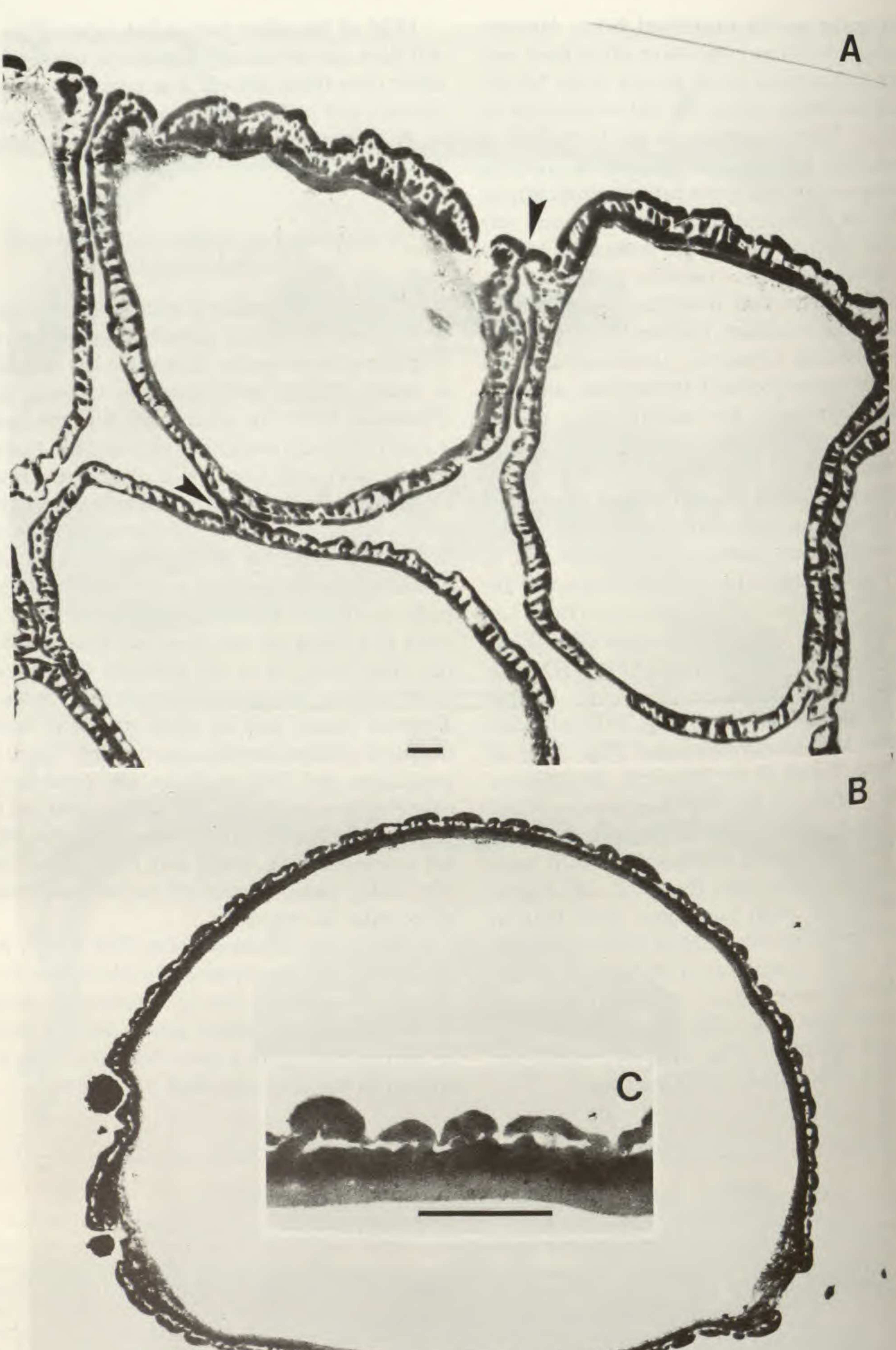

FIGURE 40. Transmission electron micrographs of Melastomataceae pollen.—A. *Tococa spadicifolia.* Section of a polyad. Fusion of tecta of two adjacent members (arrowheads). B, C. *Tococa stephanotricha.*—B. Section of an entire grain including two apertures. The tectum appears discontinuous due to the verrucate sculpturing.—C. Exine at a higher magnification. Note that foot layer and endexine are approximately equal. Scales equal 1 μm.

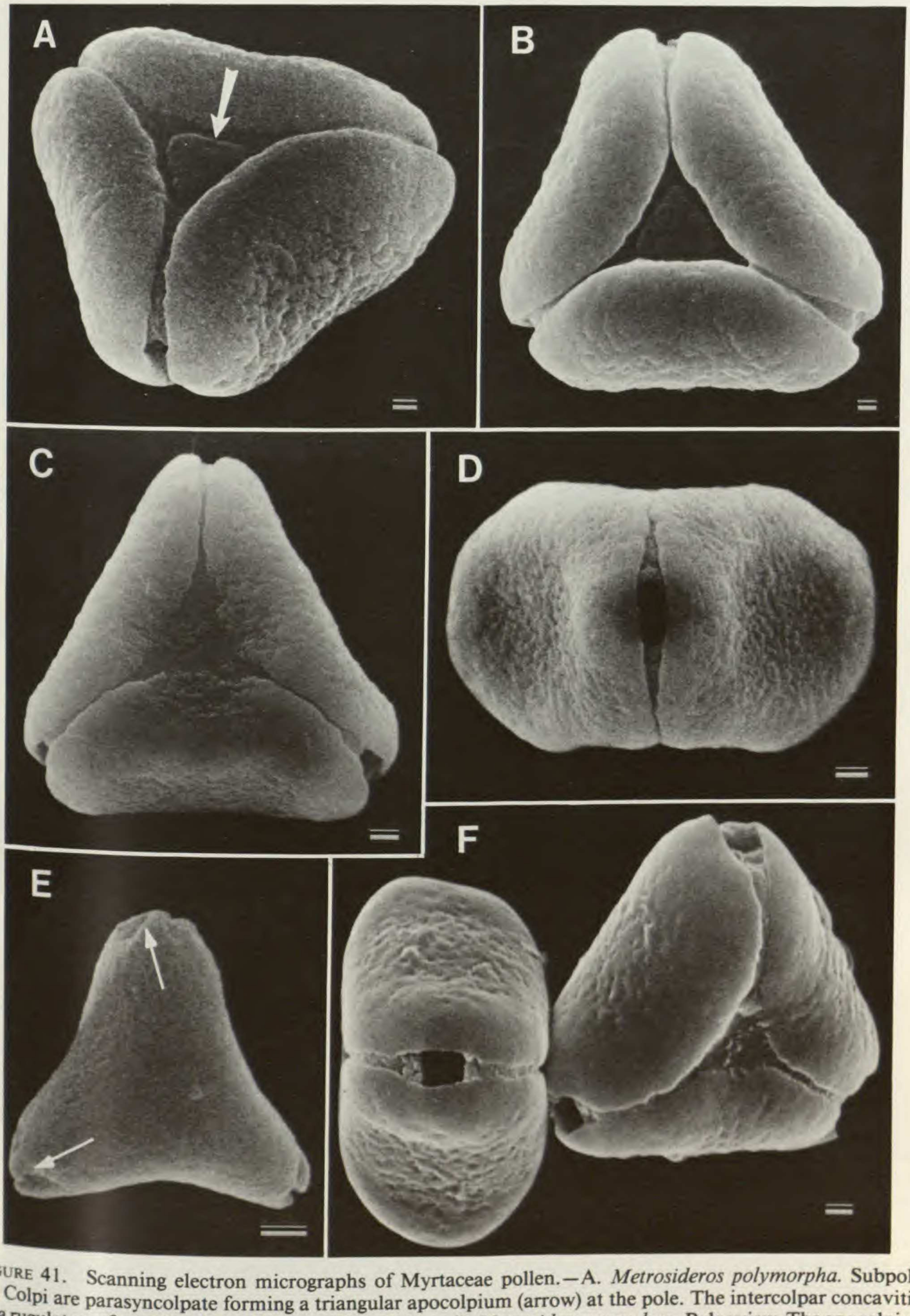

FIGURE 41. Scanning electron micrographs of Myrtaceae pollen.—A. *Metrosideros polymorpha.* Subpolar view. Colpi are parasyncolpate forming a triangular apocolpium (arrow) at the pole. The intercolpar concavities have a rugulate surface. Elsewhere the surface is smooth.—B. *Metrosideros nervulosa.* Polar view. The apocolpium and the triangular thin-walled area formed around it by the parasyncolpate colpi are somewhat collapsed. C, D. *Tristania conferta.*—C. Subpolar view. Syncolpate colpi form a thin-walled triangular area at the pole on which are scattered some granular ektexinous elements.—D. Lateral view showing the outline of a lalongate, elliptic endoaperture and two intercolpar concavities.—E. *Tristania nereifolia.* Polar view. Note the smooth-scabrate surface. The exine has irregular folds (arrows) over the apertures. Note close agreement with the scanning electron micrograph of Gadek and Martin (1981, fig. 1D).—F. *Tristania lactiflua.* Lateral (left) and subpolar (right) views. The psilate exine has punctae and channels in the intercolpar concavity areas. The grains are syncolpate. Scales equal 1 μm.

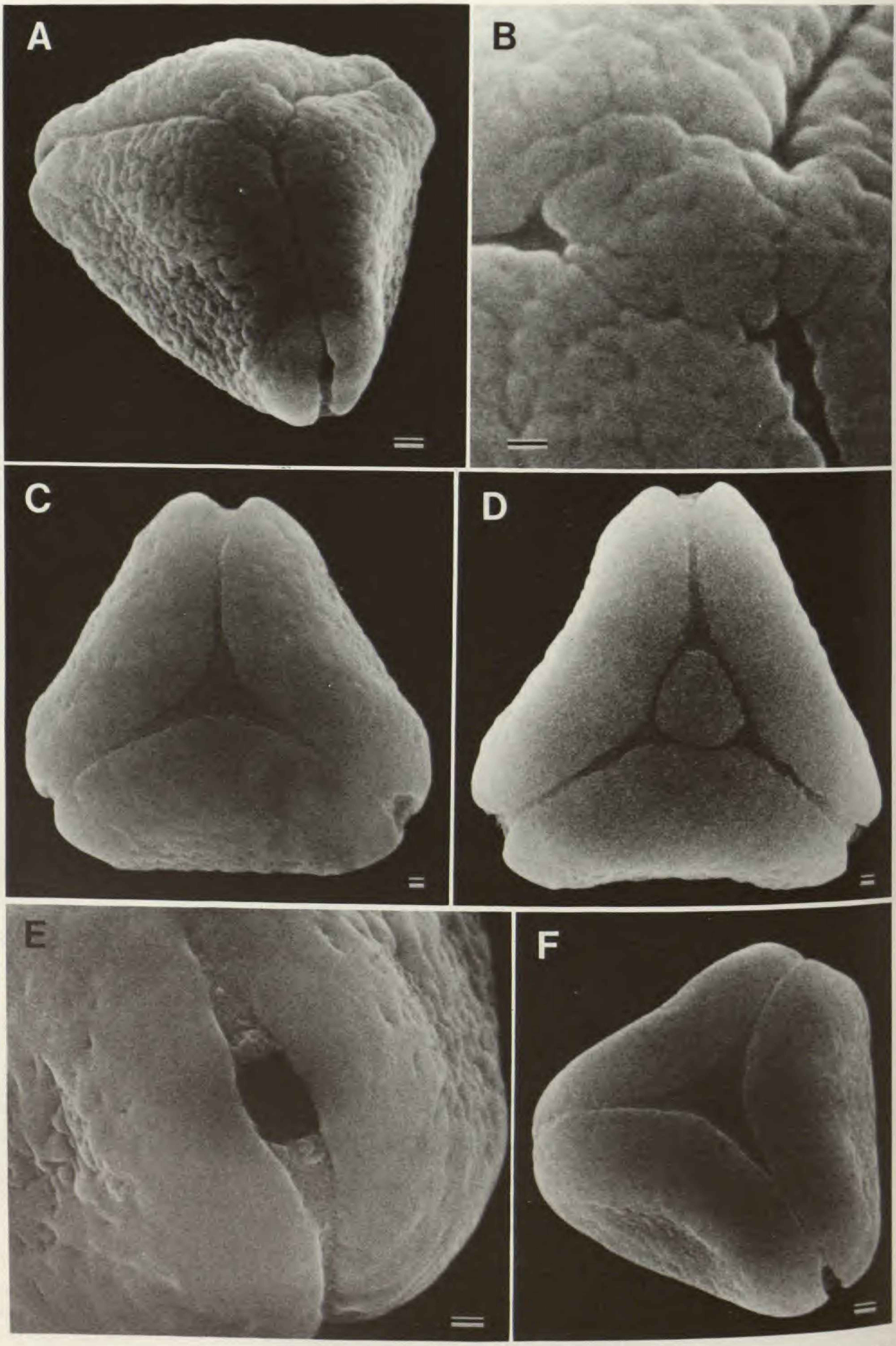

FIGURE 42. Scanning electron micrographs of Myrtaceae pollen. A, B. *Heteropyxis natalensis.*—A. Sublateral view. The surface is rugulate on the entire grain. Note distinct intercolpar concavities. The colpus at center is bifurcated at the pole and fused with the other two colpi. The latter colpi do not appear to be united with each other. Different combinations of colpi configurations, that is, syncolpate, parasyncolpate, or longicolpate, are found on different grains of *Heteropyxis.*—B. Magnified portion of an apocolpium and surrounding area. In contrast to Figure 41A, none of the colpi appear to be united at the pole. Figure 41A is similar to the scanning electron micrograph of Schmid (1980, fig. 7) except that in the latter the bulging of material at each aperture

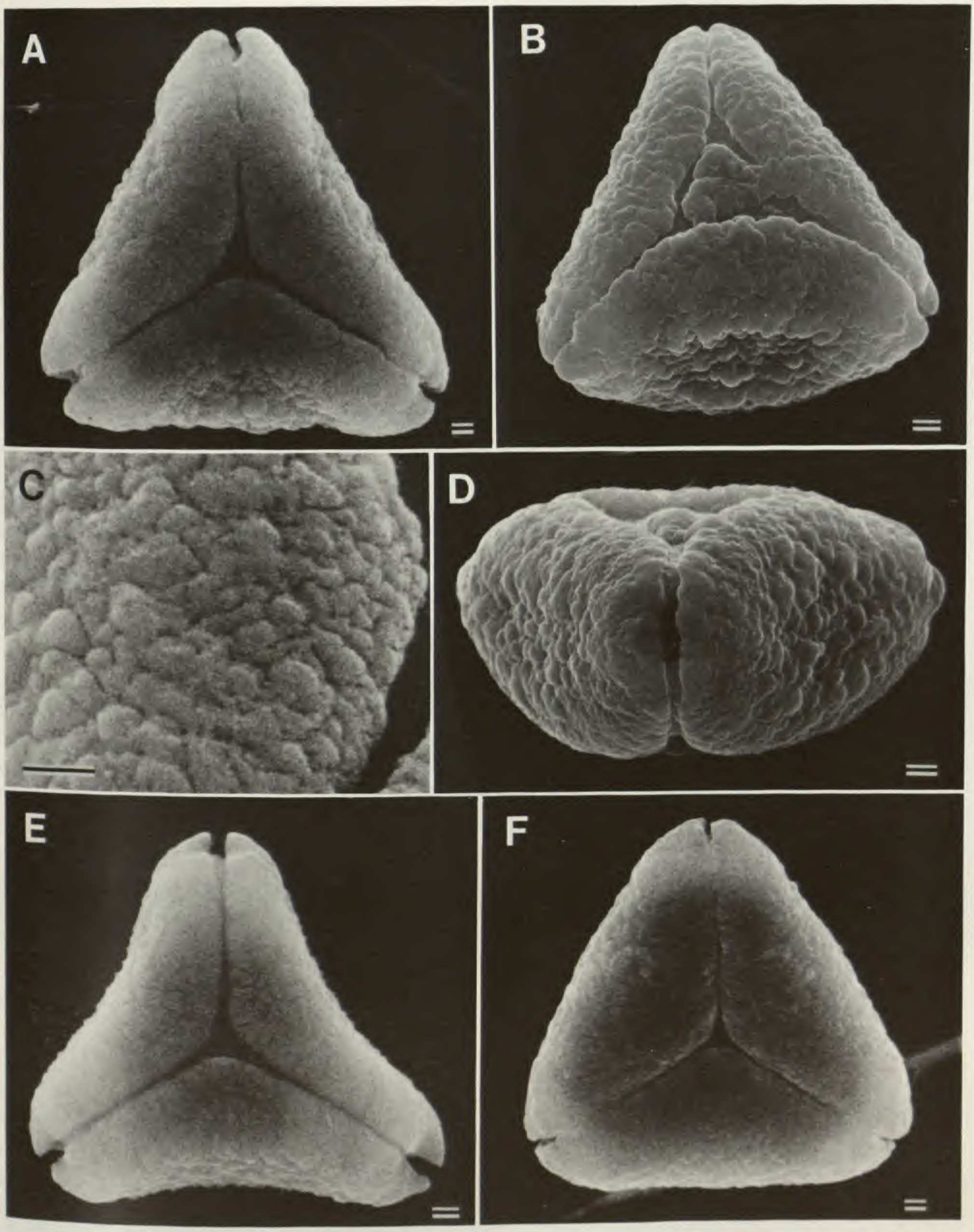

FIGURE 43. Scanning electron micrographs of Myrtaceae pollen. A, C. *Callistemon teretifolius.*—A. Polar view. Syncolpate grain. Intercolpar concavities are distinct and have a coarse rugulate-verrucate surface.—C. The mesocolpia surrounding the concavities have a fine rugulate-verrucate surface as shown here on an area near the pole. Dark areas on the right are parts of two colpi. B, D. *Callistemon citrinus.*—B. Subpolar view. The surface is rugulate. An intercolpar concavity is clearly visible (at the bottom margin). The triangular apocolpium is connected to the mesocolpium at the right (see also *Heteropyxis,* Fig. 42A).—D. Lateral view showing two intercolpar concavities.—E. *Calothamnus validus.* Polar view. The smooth surface has fine channels. The intercolpar concavities are granular-verrucate.—F. *Eremaea pauciflora.* Polar view. Intercolpar concavities appear to be absent. The surface is more or less uniform on the entire grain with fine granular, verrucate, rugulate elements. Scales equal 1 μm.

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probably represents the cytoplasmic contents of the unacetolyzed (?) pollen grain. C–E. *Eucalyptus ficifolia.*—C, D. Polar views of two grains from the same sample. In C the grain is syncolpate, in D it is parasyncolpate.—E. Magnified area near the equator (and endoaperture).—F. *Eucalyptus robusta.* Subpolar view. Syncolpate grain. Intercolpar concavities have a granular surface. Elsewhere the surface is smooth. Scales equal 1 μm.

(1) Longicolpate type

The colpi are long; "colporate grains are longicolpate when the colpi are longer than the distance between their apices and the poles" (Pike, 1956: 51). *Hypocalymna angustifolium* (Fig. 44E, G), *Myrceugenella apiculata* (Fig. 47F), and *Ugni molinae* (Fig. 46D, E) belong to this type. In addition to the long colpi, pollen shape is also similar in *Myrceugenella* and *Ugni*: the triangular grains have convex sides and slightly protruding apertures in polar view and an elliptic shape with acute ends in lateral view. The surface in *Myrceugenella* is verrucate-granular with some larger verrucate elements at the poles (Fig. 47F). *Ugni* shows a unique surface pattern with multiangular units that have acute corners (Fig. 46E). These units are large and scattered at the poles but become smaller and more tightly packed toward the equator. The surface appears to be granular around the endoapertures. In *Hypocalymna,* the grains are triangular with straight sides in polar view and elliptic with acute corners in lateral view. The surface has a pebbly appearance, with large units of different shapes, separated by deep, narrow spaces. This pattern becomes finer at the margins of the colpi and at the poles. The colpi in all three taxa are very narrow, with a smooth surface except in *Myrceugenella* which has a granular surface.

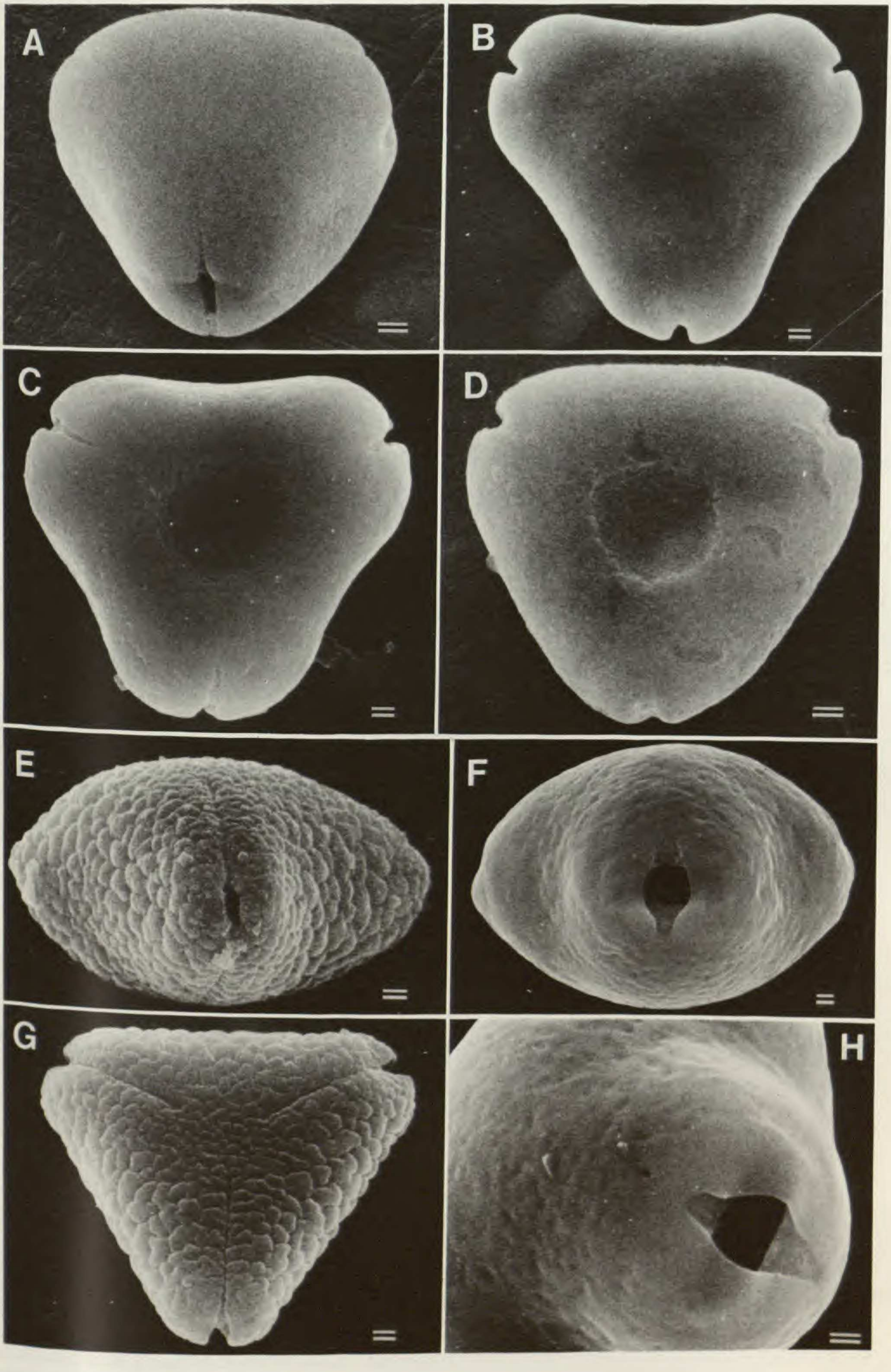
(2) Syncolpate and parasyncolpate type

In syncolpate grains, the colpi are either straight, that is, meeting at the poles without becoming wider, or curved where they are wider at the poles and form a triangular area. In parasyncolpate grains, the colpi bifurcate at the poles and their branches meet and outline a triangular apocolpium. Not all grains are strictly syncolpate or parasyncolpate; some are syncolpate on one pole and parasyncolpate on the other pole (i.e., syn/para), while others also combine with longicolpate grains and result in long/syn and long/para forms. These combinations were found in *Myrtus communis, Psidium littorale, Eucalyptus ficifolia* (Fig. 42C, D), *E. robusta, Heteropyxis natalensis, Temu divaricatum,* and *Eugena elliptifolia.* The taxa included in the syncolpate and parasyncolpate type are further grouped according to the presence or absence of intercolpar concavities.

Pollen with intercolpar concavities. Since the Myrtaceae pollen examined is oblate in lateral view, the intercolpar concavities are equatorially elongated and elliptic in shape. They are clearly defined in *Acmena smithii* (Fig. 47B), *Callistemon citrinus* (Fig. 43B, D), *C. teretifolius* (Fig. 43A), *Calothamnus validus* (Fig. 43E), *Eucalyptus ficifolia* (Fig. 42C–E), *E. robusta* (Fig. 42F), *Heteropyxis natalensis* (Fig. 42A, B), *Melaleuca hypericifolia* (Fig. 45A, B), *M. rhaphiophylla* (Fig. 45E), *Tristania conferta* (Fig. 41C, D), and *T. lactiflua* (Fig. 41F). In *Cleistocalyx operculata* (Fig. 47A), *Eugenia elliptifolia* (Fig. 47D), *Metrosideros nervulosa* (Fig. 41B), and *M. polymorpha* (Fig. 41A) they are not as markedly "depressed" as in the above mentioned taxa. In *Acmena, Eucalyptus ficifolia, E. robusta,* and *Tristania lactiflua,* the intercolpar concavities have many punctae with fine, irregular channels on a smooth surface while the surrounding areas of the mesocolpia are psilate. Similar surface sculpturing is present in *Eugenia elliptifolia* and *Cleistocalyx. Melaleuca hypericifolia* has a verrucate-granular surface in the intercolpar concavities and the surrounding areas are scabrate. In *Callistemon teretifolius, C. citrinus,* and *Heteropyxis,* the surface of the mesocolpia is rugulate, and it is regulate-verrucate in the intercolpar concavities. In *Melaleuca rhaphiophylla, Tristania conferta,* and perhaps *Calothamnus* (Fig. 43E) it is granular-verrucate in the intercolpar concavities and finely rugulate with fine channels on the mesocolpia. In *Metrosideros nervulosa* and *M. polymorpha* the intercolpar concavities have a coarse, rugulate-verrucate surface. On the mesocolpia, it is finely rugulate in the former and psilate in the latter (Fig. 41A, B).

Pollen without intercolpar concavities. Here, the surface is more or less uniform over the entire

FIGURE 44. Scanning electron micrographs of Myrtaceae pollen.—A. *Baeckea virgata.* Sublateral view. The surface is psilate, colpi are short.—B. *Homoranthus wilhelmii.* Polar view showing a psilate surface.—C. *Balaustion microphyllum.* Polar view. Psilate surface, short colpi. Note the circular, thin-walled area at the pole.—D. *Thryptomene calycina.* Polar view. Similar to C. E, G. *Hypocalymna angustifolium.*—E. Lateral view. Surface is pebbly, rugulate-verrucate.—G. Polar view. The grain is longicolpate. F, H. *Chamaelaucium uncinatum.*—F. Lateral view. The surface is smooth and with pits. The colpus is short and wide.—H. Close-up of the aperture. Colpus is shorter than the lalongate, elliptic endoaperture below it. Scales equal 1 μm.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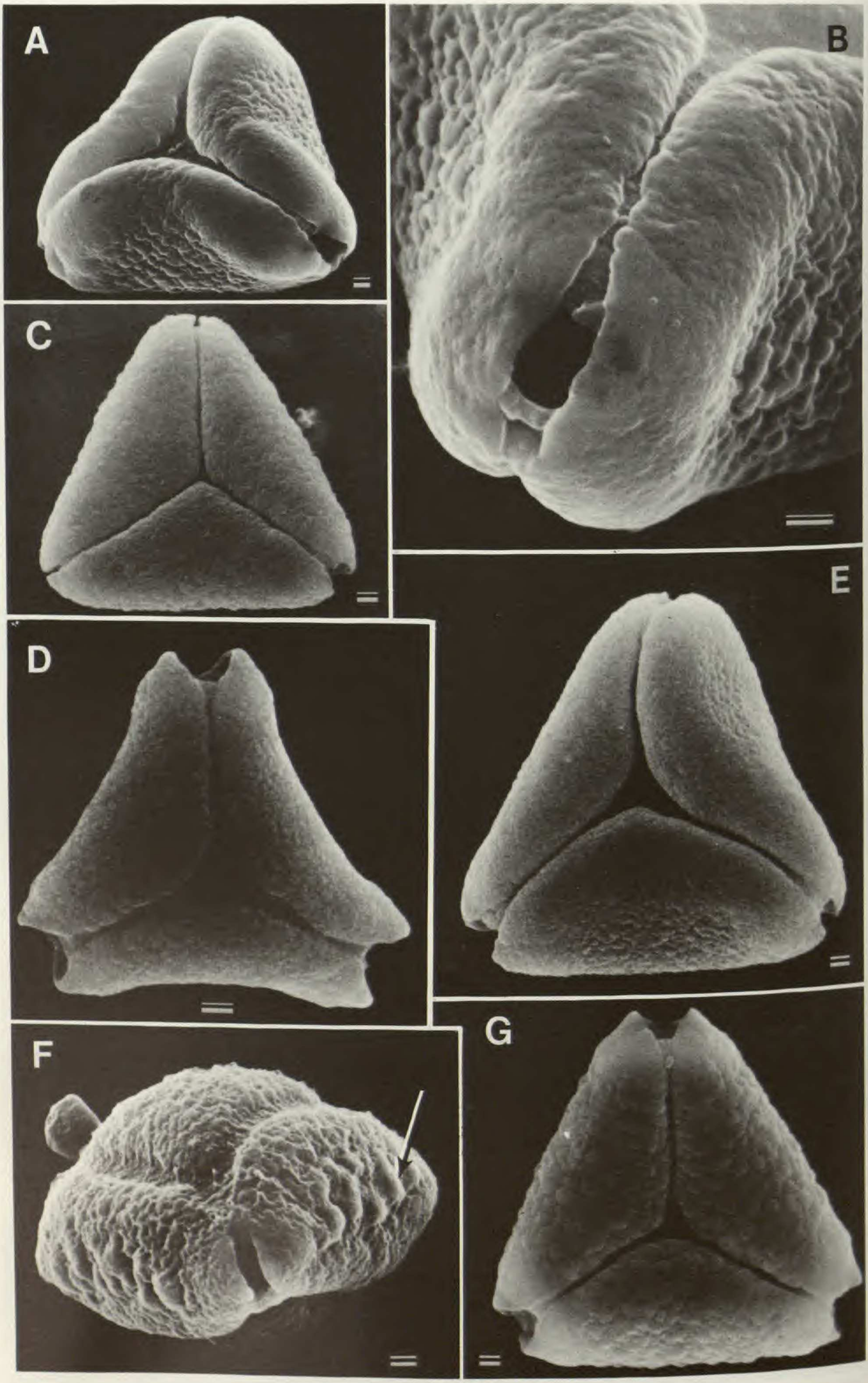
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grain. The surface in *Myrtus communis* (Fig. 48B–D), *Psidium littorale* (Fig. 46A–C), *Eremaea pauciflora* (Fig. 43F), *Melaleuca preissiana* (Fig. 45D), and *M. decussata* (Fig. 45C) is similar: granular-verrucate-rugulate. There are fine, branched, irregular channels separating the surface elements. In *M. communis* (Fig. 48C), minute lines and dots are seen on the surface elements.

The surface in *Luma chequen* (Fig. 47E), *Pilidiostigma glabrum* (Fig. 46F), and *Rhodamnia argentea* (Fig. 48E) is verrucate-granular. In *Luma,* the colpi are curved and form a large thin-walled triangular area at the poles that has irregularly scattered verrucae and granules on it. In *Pilidiostigma,* at the parasyncolpate pole, scattered granules form a triangular apocolpium. The surface is smooth near the endoapertures in both of these taxa. In *Rhodamnia,* larger verrucate elements are present along the margins of the mesocolpia, even near the endoapertures.

Austromyrtus bidwillii (Fig. 48F), *Temu divaricatum* (Fig. 48A), *Melaleuca pulchella* (Fig. 45G), and *Psiloxylon mauritianum* (Fig. 45F) show a coarsely rugulate pattern. In *Austromyrtus,* isolated rugulate and verrucate elements are present on the apocolpia. In *Psiloxylon,* the rugulate elements are larger on the equator. This genus has large apocolpia and differs from the rest of the parasyncolpate taxa in this respect. *Eugenia capuli* (Fig. 47C) has a slightly less coarse rugulate surface. In all the rugulate taxa, the surface near the endoapertures is smooth.

In TEM, the cross section of the *Myrtus communis* monad (Fig. 49C, D) shows that the endexine is uniform except near the endoapertures where it increases in thickness and becomes granular. The thin foot layer has an irregular upper margin and is discontinuous. The short columellae support a thick, infratectal granular layer. The tectum is also thick, with an irregular upper margin, and shows many perforations. The section of the tetrad (Fig. 49A) indicates in places a discontinuous dome-shaped tectum with a granular layer below it. Figure 49B shows the fusion of tecta between two members of the tetrad.

(3) *Brevicolpate and brevissimicolpate type*

In the brevicolpate grains the length of the colpi is equal to or less than the distance between their ends and the poles (Erdtman, 1971). In the brevissimicolpate grains, the colpus length is less than that of the underlying endoaperture (Erdtman, 1971). *Chamaelaucium uncinatum* (Fig. 44F, H) has brevissimicolpate grains. The surface is smooth with minute pits. The ends of the very short colpi are rounded.

(4) *Uncertain type*

Due to the lack of sufficient data the following taxa could not be assigned to any of the above pollen types. *Baeckea virgata* (Fig. 44A) and *Osbornia octodonta* (Fig. 46G) appear to have curved syncolpi. However, they are often partially obscured or not well developed and then appear as short colpi which outline a faint triangular thin-walled area at the pole. Moreover, *Baeckea* appears to have intercolpar concavities. *Homaranthus wilhelmii* (Fig. 44B) and *Thryptomene calycina* (Fig. 44D) seem to be brevissimicolpate. The surface is psilate in both taxa and *Thryptomene* shows a circular, thin-walled area at the pole. *Balaustion microphyllum* (Fig. 44C) appears to be brevicolpate with a psilate surface and a circular, thin-walled area on the pole. Intercolpar concavities may be present. *Tristania nereifolia* (Fig. 41E) differs from all the taxa of the family. The triangular pollen has

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FIGURE 45. Scanning electron micrograph of Myrtaceae pollen. A, B. *Melaleuca hypericifolia.*—A. Sublateral view. Distinct intercolpar concavities have a verrucate-granular surface. Elsewhere the surface is psilate. Colpi are curved (arcuate) and united at the pole.—B. View near the endoaperture.—C. *Melaleuca decussata.* Polar view. The fine granular-verrucate-rugulate surface sculpture is essentially uniform over the entire grain. In contrast to A the colpi are straight and united at the pole. Intercolpar concavities are absent.—D. *Melaleuca preissiana.* Polar view. The surface is fine granular-verrucate-rugulate and more or less uniform over the entire grain. Colpi are curved (see A). Intercolpar concavities are absent.—E. *Melaleuca rhaphiophylla.* Subpolar view. The intercolpar concavities are not as distinct as in *M. hypericifolia.*—F. *Psiloxylon mauritianum.* Lateral view. The syncolpi form large apocolpia on both poles. The arrow indicates coarse rugulate elements on the equator: this is not believed to be a regular characteristic as other grains of *Psiloxylon* have an essentially uniform sculpture. Comparison should be made with the scanning electron micrograph of Schmid (1980, fig. 5).—G. *Melaleuca pulchella.* Polar view. Surface is rugulate. Scales equal 1 μm.

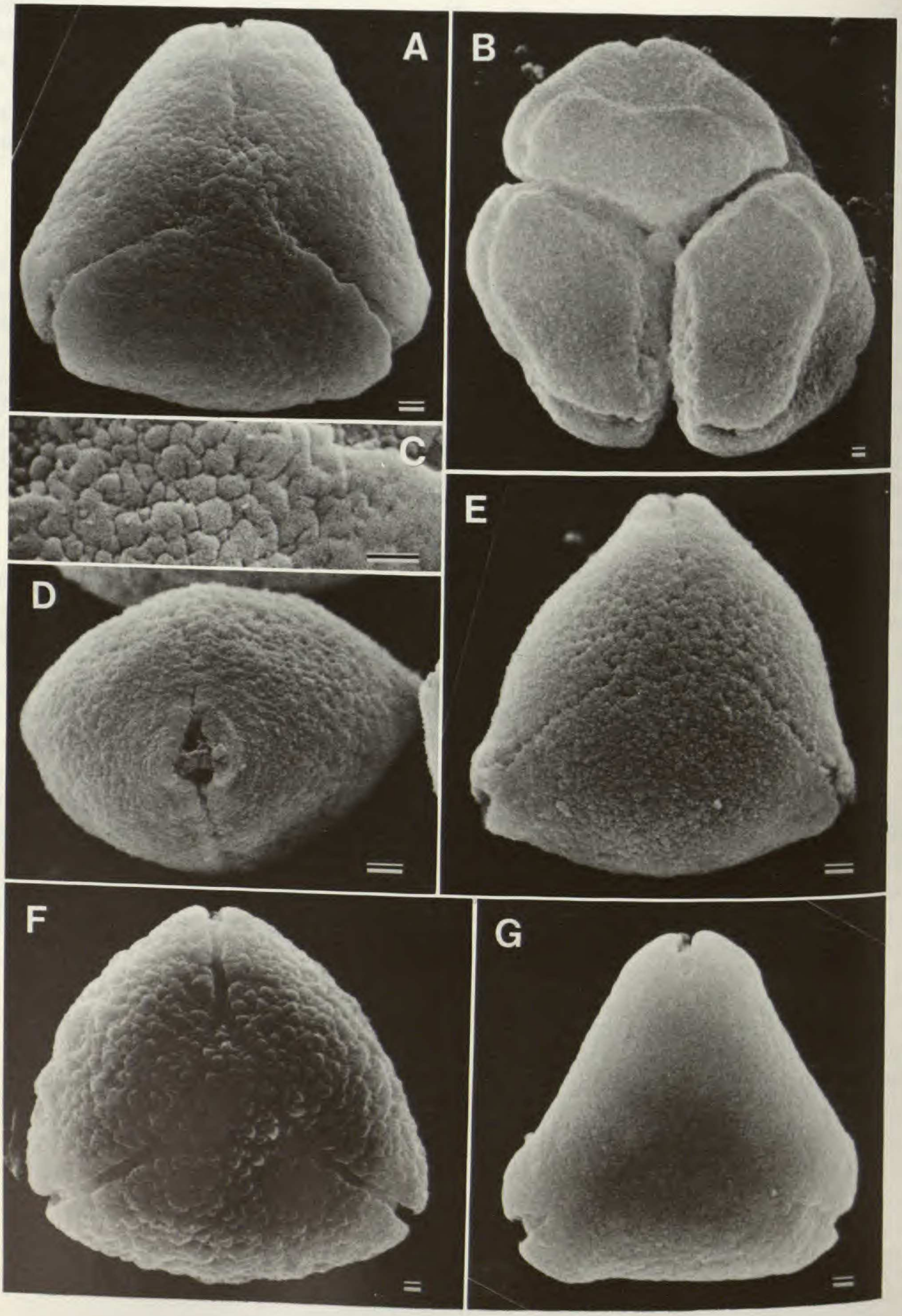

FIGURE 46. Scanning electron micrographs of Myrtaceae pollen. A–C. *Psidium littorale.*—A. Subpolar view of a monad. The grain is longicolpate (parasyncolpate and syncolpate grains are also present in sample). Intercolpar concavities are absent.—B. A tetrahedral tetrad (fourth grain is at the back).—C. Surface details of A near the pole showing the surface to be granular-verrucate-rugulate. D, E. *Ugni molinae.*—D. Lateral view showing elliptic shape.—E. Polar view. Colpi are long. Note angular surface elements near the pole.—F. *Pilidiostigma glabrum.* Polar view. The surface is verrucate-rugulate. The arcuate colpi are parasyncolpate. The apocolpium

deeply concave sides. The surface is scabrate and the nature of the three apertures is difficult to interpret but the pollen appears to be triporate.

Discussion

In his extensive bibliography of myrtalean palynology, Thanikaimoni (1984) lists only three references that allude to electron microscopy of Myrtaceae pollen, making it obvious that SEM-TEM investigations are greatly needed in the family, although, as discussed below, taxonomic investigations by Gadek and Martin (1981, 1982) are currently in progress. Since our intent in this study is the presentation of a broad overview of the Myrtales core families we shall not attempt a review of the extensive Myrtaceae pollen references, but shall only briefly mention a few of the more recent/pertinent ones. The most comprehensive taxonomic light microscope study was that of Pike (1956), which included 71 genera and 300 species from the southwestern Pacific area. Some of the conclusions reached from this study were:

(1) although the pollen in Myrtaceae is essentially uniform, in some taxa minor differences make it possible to recognize particular genera or species;

(2) within the family (following Niedenzu's classification, 1893) "There appears to be no particular feature that separates pollen of the Myrtoideae from that of the Leptospermoideae, but pollen of the tribe Chamaelaucieae (placed by Niedenzu in the Leptospermoideae) differs markedly from that of all other tribes in the family" (Pike, 1956: 46);

(3) within a tribe the taxa usually are similar, ". . . e.g., Myrtinae, Chamaelaucieae, but it is possible for closely related genera to have quite distinct pollen, e.g., *Metrosideros* and *Spermolepis, Leptospermum* and *Agonis, Baeckea* and *Balaustion, Wehlia* and *Pileanthus.* On the other hand, grains of widely separated genera may show certain similarities, e.g., those of *Regelia ciliata* are difficult to distinguish from those of some species of *Eucalyptus,* and those of *Astartea* and *Agonis* are ± similar" (Pike, 1956: 46);

(4) "grains of different species of the same genus are usually indistinguishable, e.g., *Leptospermum,* or they may be similar in general features but show a comparatively large range in size, e.g., *Eucalyptus.* Rarely is it possible to make specific distinctions as in *Regelia*" (Pike, 1956: 47).

McIntyre (1963) examined the pollen of 18 New Zealand taxa and found that most genera could be recognized. Species within genera also could be recognized to some extent. As concerns fossil identification of Myrtaceae pollen, McIntyre (1963: 104) stated: "There is little or no difference between the pollen grains of many genera of the Myrtaceae. Identification of living genera and species from fossil pollen, therefore, can only be reliable if there are no grains of similar type, from extinct genera and species, in the sample under consideration . . . . When all factors are considered it is obvious that attempted identifications of fossil Myrtaceae pollen on the basis of pollen characters of the indigenous species should be restricted to a period of time where it is reasonably certain that no other species or genera of the family were present . . . ."

Most recently Gadek and Martin (1981) examined the pollen of 28 species and seven genera of subtribe Metrosiderinae with light microscope and SEM. They found a greater range of pollen morphology within the family than was heretofore recognized and in some instances pollen could be identified to the generic and specific levels. With the SEM they were also able to circumscribe three basic exine sculpture types: (1) Psilate to microscabrate, (2) microfossulate, and (3) microrugulate, rugulate.

Lugardon and van Campo (1978) examined pollen of *Tristania laurina* and *Myrtus communis* with TEM and apparently encountered, at least with the latter, the same problem as we did, that is, a lack of staining contrast between the endexine and the foot layer. They described the thin, often discontinuous foot layer above a "white line" and a thick endexine below it as constituting the nexine. They further described an infractectal granular layer between the tectum and nexine but did not recognize columellae. In contrast, our section of *M. communis* (Fig. 49D) indicates very short columellae below the infractectal granular layer. This section also shows a distinct foot layer and endexine. The most de-

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← is formed by scattered verrucate, granular elements.—G. *Osbornia octodonta.* Polar view. The surface appears to be scabrate, colpi are short and at the pole form a weakly developed thin-walled triangular area. Scales equal 1 μm.

finitive TEM study is that of Gadek and Martin (1982: 75), in which pollen of *Eucalyptus* and *Tristania* were examined in great detail. Their general description for the pollen structure is as follows: "The species all show a typical angiosperm exine differentiation consisting of two chemically different layers, an electron dense ektexine and a less dense endexine divided by a very thin electron-transparent lamella. They all differ, however, from the typical angiosperm architecture by the presence of a somewhat unstructured, granulate infratectal layer and the presence of a granular/alveolate endexinous layer around the pores. Species differences relate to the granulate/columellate organization of the infratectal layer; the extent or density of tectal perforations; and the presence and thickness of a foot-layer around the grain."

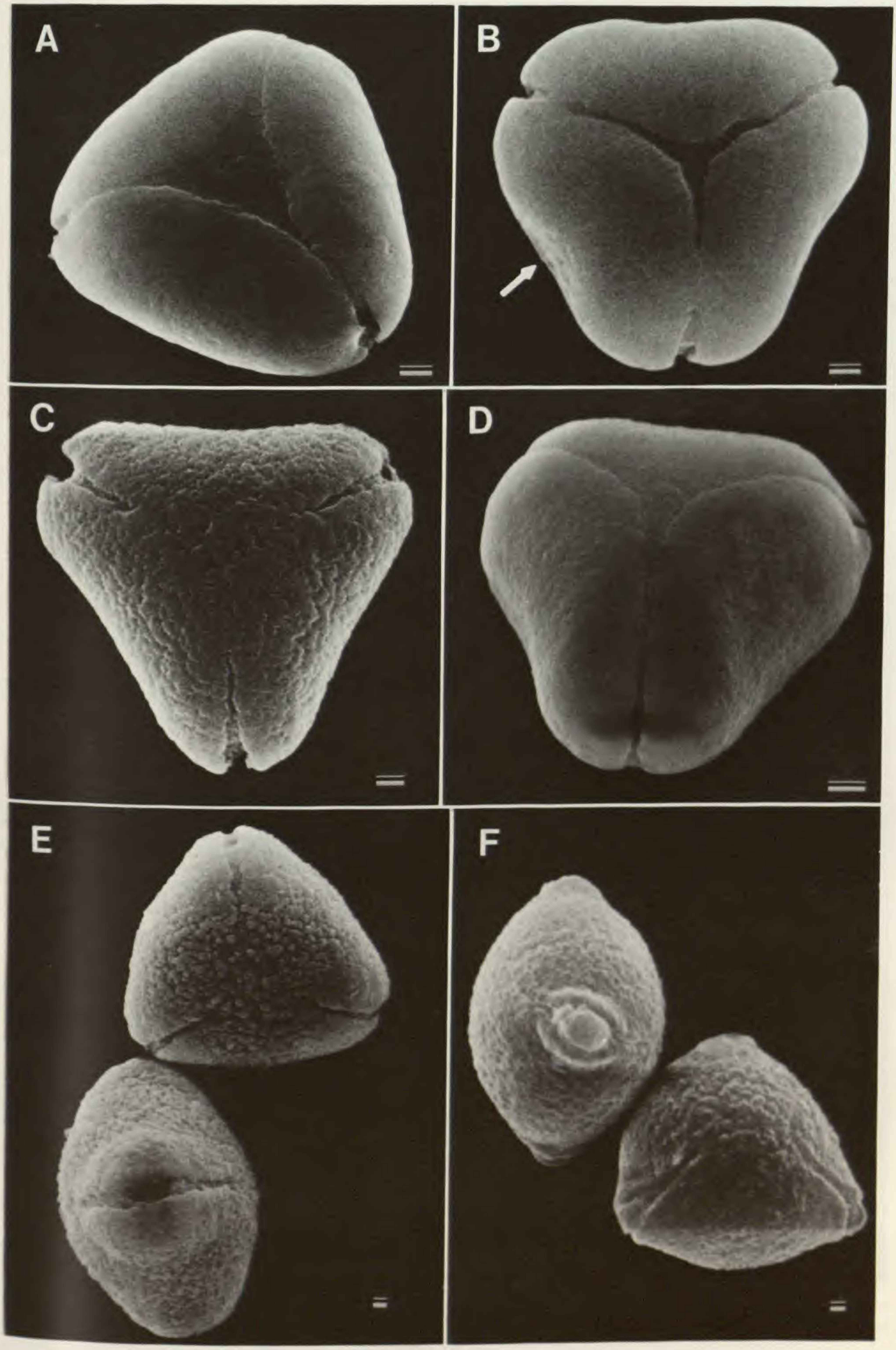
Dahlgren (in Dahlgren & Thorne, 1984) regards both *Heteropyxis* and *Psiloxylon* as segregate monotypic families. *Psiloxylon* differs from other parasyncolpate taxa of Myrtaceae by having unusually large apocolpia and larger rugulate elements on the equator, but otherwise is similar to the rest of the family. *Heteropyxis* is not easily distinguished from other genera in the syncolpate and parasyncolpate group with intercolpar concavities.

In summary, Myrtaceae pollen as documented with SEM does not appear to have any close similarities to taxa from the other core families of the Myrtales. Perhaps some superficial similarity exists with Onagraceae pollen but there is no mistaking the two families. Erdtman (1971) suggests similarity to Lythraceae (perhaps through *Cuphea*) but we have not been able to confirm it in this study. Furthermore, we do not have sufficient data to compare Myrtaceae pollen with families outside of the Myrtales as suggested by Erdtman (1971). It would be of interest to examine pollen of Cunoniaceae, Proteaceae, Lecythidaceae, and Sapindaceae in order to check Erdtman's (1971) observations. Pollen of Lecythidaceae and Sapindaceae have been examined in SEM (Muller, 1972, 1973; Muller & Leenhouts, 1976; Mori et al., 1980) and are not similar to Myrtaceae pollen. However, in Sapindaceae there are several taxa with triangular, parasyncolpate grains (Muller & Leenhouts, 1976).

FIGURE 47. Scanning electron micrographs of Myrtaceae pollen.—A. *Cleistocalyx operculata*. Subpolar view. The psilate surface has punctae and channels in the shallow and barely discernible intercolpar concavity areas.—B. *Acmena smithii*. Polar view. Surface is psilate; punctae and channels are present in the intercolpar concavities (arrow).—C. *Eugenia capuli*. Polar view of the convex face of the grain, the opposite face is concave. The surface is rugulate. Colpi are united (i.e., syncolpate) but are obscured by rugulate elements at the pole. The pole on the concave face usually has more distinct syncolpi.—D. *Eugenia elliptifolia*. Sublateral view showing syncolpi. The psilate surface becomes coarser and has fine channels and punctae in the intercolpar concavities.—E. *Luma chequen*. Polar (upper) and lateral (lower) views. The surface is smooth to slightly coarse in the area of the endoapertures. Toward middle part of the mesocolpia it becomes granular-verrucate. There is a large thin-walled area at the poles that has granules and verrucae scattered over it. The colpi merge with this thin-walled area, thus, the grains are syncolpate.—F. *Myrceugenella apiculata*. Lateral (left) and subpolar (right) views of unacetolyzed, glutaraldehyde-fixed pollen. The surface is granular-verrucate. Colpi are long. Scales equal 1 μm.

FIGURE 48. Scanning electron micrographs of Myrtaceae pollen.—A. *Temu divaricatum*. Polar view of a parasyncolpate grain. Other colpi combinations were found in the same sample. The surface is rugulate. B–D. *Myrtus communis*.—B. Polar view of a monad. All colpi are not united at this pole but different colpi combinations (i.e., parasyncolpate/syncolpate; syncolpate/syncolpate, etc.) are found within the same sample.—C. In this enlarged view of the surface, rugulate and verrucate elements contain fine electron dense lines and dots.—D. Tetrahedral tetrads are also common in the sample.—E. *Rhodamnia argentea*. Polar view. The syncolpate grain has straight colpi. The surface is verrucate-granular. Large verrucate-rugulate elements are present on colpi margins and at the pole.—F. *Austromyrtus bidwillii*. Subpolar view. Parasyncolpate grain shows rugulate surface. The apocolpium is formed by separate rugulate and verrucate elements. Scales equal 1 μm.

FIGURE 49. Transmission electron micrographs of Myrtaceae pollen. A–D. *Myrtus communis*.—A. Section of three members of a tetrahedral tetrad. The proximal faces of the grains have a discontinuous tectum (due to verrucate-granular sculpture), while the distal faces show a more or less continuous tectum. In the grain on the left, the apocolpium (the thin-walled triangular area where colpi unite) shows a thickened endexine (en). Several ektexinous connections (arrows) between adjacent grains are visible.—B. A close-up of a portion of A showing fusion of tecta.—C. Cross section of a single grain passing through the three apertures near the equator.—D. An enlarged area of C showing a thick tectum, an infratectal granular layer, short columellae, a thin discontinuous foot layer, and a well-developed endexine. The transmission electron micrograph of Lugardon and van Campo (1978, Pl. 1, figs. 1–6) differs from C and D in that columellae were not recognized. Scales equal 1 μm.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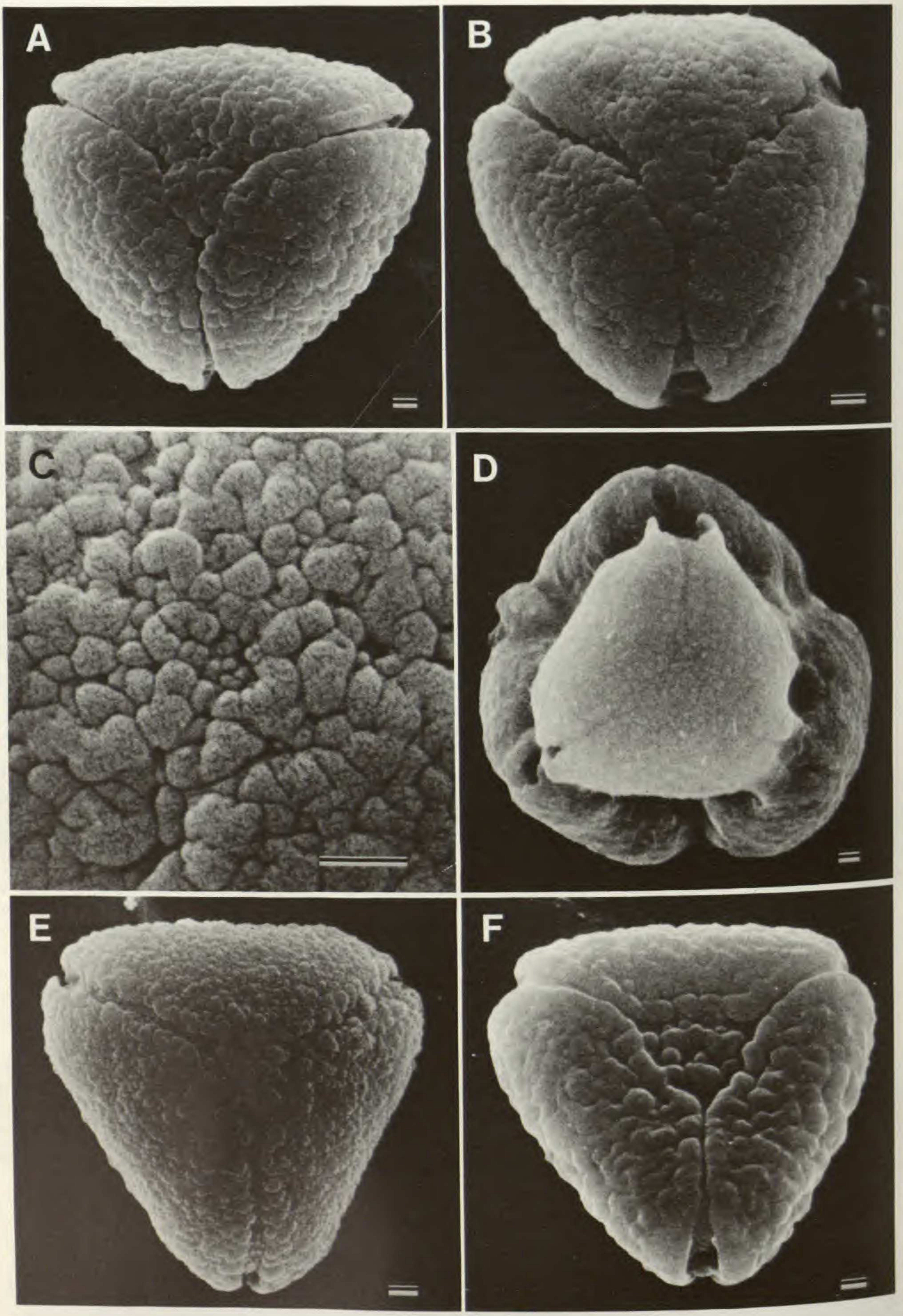
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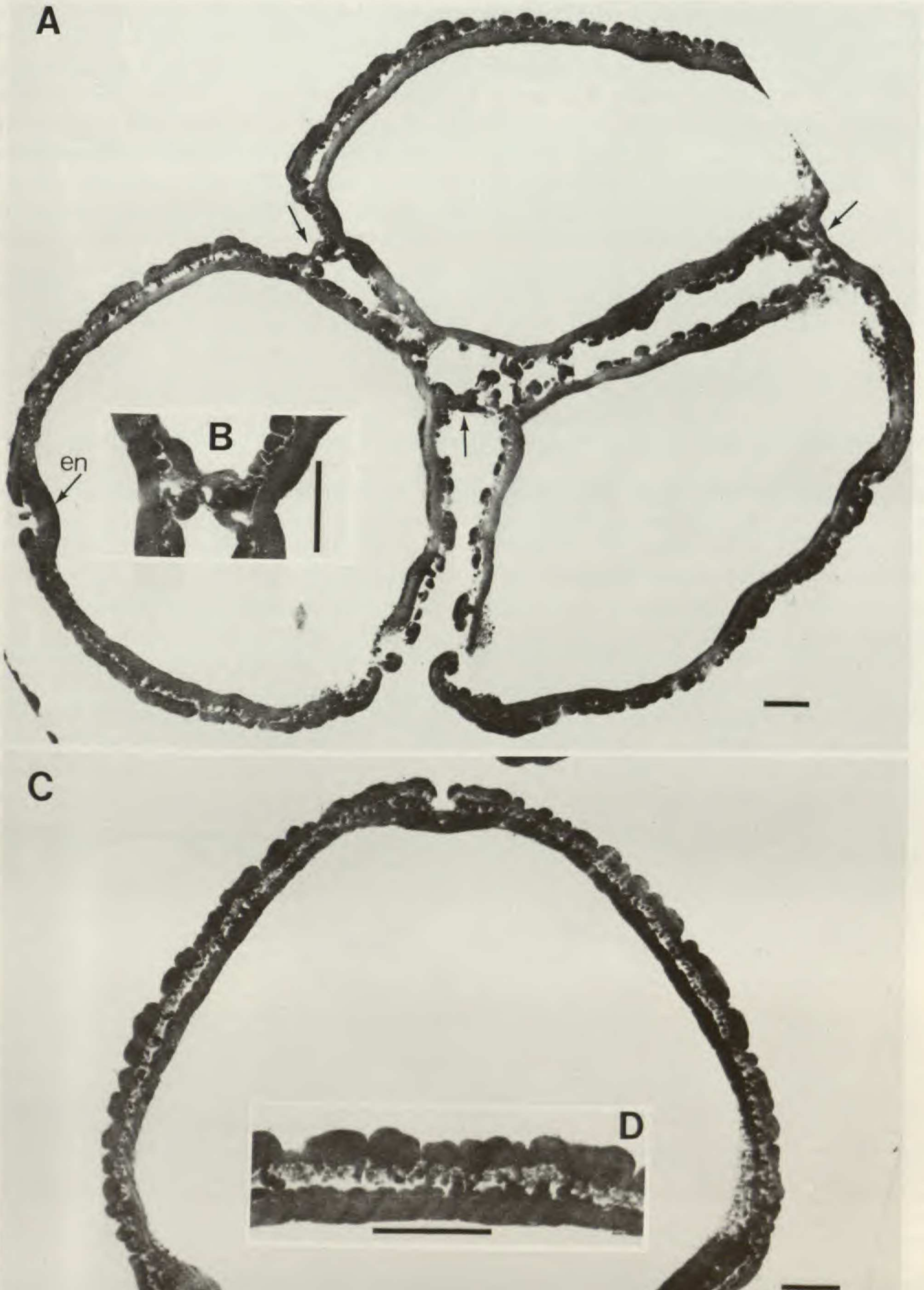
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The distinct SEM appearance of Myrtaceae pollen is countered by the TEM structure, which basically conforms with a typical post-and-beam organization of angiosperm pollen. The 'granular/alveolate' endexine of Gadek and Martin (1982) does appear somewhat similar to Onagraceae pollen but as further suggested by them it can also be found in other families, thus diminishing the uniqueness of the character. Furthermore, the infratectal granular layer has been observed in a number of core families in this study.

ONAGRACEAE

The scanning and transmission electron micrographs of Onagraceae pollen in Figures 50–63 and the data in Table 2 are intended as a general overview of the morphology of the family (forthcoming studies with Nowicke & Praglowski will be more inclusive). Pollen characterized by a dominant central body (Praglowski et al., 1983) with markedly protruding apertures is typical of *Fuchsia* (Fig. 50A, B), *Circaea* (Fig. 50C, D), *Clarkia* (Fig. 52A, B, D), *Gaura* (Figs. 52H, 53 A, B), *Heterogaura* (Fig. 54A, B), *Calylophus* (Fig. 55A, B), *Stenosiphon* (Fig. 55E), and *Oenothera* (Fig. 56A, C). In comparison, the apertural protrusions are less pronounced in *Xylonagra* (Fig. 54E, F), *Camissonia* (Fig. 57), *Ludwigia* (Fig. 58F, H), and *Hauya* (Fig. 50E), while in *Lopezia* (Fig. 51A, B, D, G), *Gayophytum* (Fig. 53E, F), *Gongylocarpus* (Fig. 56D), *Boisduvalia* (Fig. 58A), and *Epilobium* (Fig. 59A, B, E, J), the apertures are non-protruding. These latter genera, particularly *Lopezia* (Fig. 51A, D), have a triangular outline in polar view. While most Onagraceae pollen is three-aperturate, that of *Fuchsia* (Fig. 50A) is also characteristically two-aperturate in certain sections (Praglowski et al., 1983; Nowicke et al., 1984). Four-aperturate grains, as depicted for *Lopezia* (Fig. 51G) and *Heterogaura* (Fig. 54B), are less commonly represented, although occurring in many genera of the family.

Most genera of Onagraceae shed their pollen exclusively as monads, but some also shed the pollen in tetrads or polyads. Pollen tetrads characterize *Boisduvalia* (Fig. 58A), most species of *Epilobium* (Fig. 59E, J), and some species of *Camissonia* (Fig. 57A, F–H) and *Ludwigia* (Fig. 58A, F). In *Epilobium brachycarpum* (*E. paniculatum*), most individuals shed their pollen as monads (Fig. 59A, B), as do all species of sect. *Chamaenerion* (cf. Raven, 1976), while a few individuals are known to shed the pollen in tetrads (Fig. 59E), as do all other species of *Epilobium*. Polyads are found only in some species and sections of *Ludwigia* (Praglowski et al., 1983), including *L. longifolia* (Fig. 58H) in this study. The internal bridges (Fig. 58G) connecting adjacent tetrad members and the external bridges (Fig. 58I) connecting adjacent tetrads appear identical to each other as well as to their respective exine surfaces.

All taxa except *Circaea alpina* subsp. *imaicola* (Fig. 50D) are characterized by long ektexinous

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FIGURE 50. Scanning electron micrographs of Onagraceae pollen.—A. *Fuchsia thymifolia* subsp. *thymifolia*. Oblique lateral view with viscin threads associated with the proximal (top) pole. The arrow indicates a thickened area of threads showing a segmented-ropy morphology characteristic of this species (see Skvarla et al., 1978, Pl. 4, fig. 6). The apertural protrusion (AP) extends from the central body (CB). A portion of a second apertural protrusion is visible at the upper left. This two-aperturate condition is characteristic for the pollen of many species of *Fuchsia*.—B. *F. michoacanensis*. Apertural protrusion with crack extending from pore (at right) into the central body. The arrow indicates endexine lamellae. The exine surface consists of rod-like to elongate (almost rugulate) elements.—C. *Circaea cordata*. Portion of a pollen grain with apertural protrusion and a single smooth viscin thread. The surface is composed of globular and rod-like elements.—D. *C. alpina* subsp. *imaicola*. Lateral view showing three apertural protrusions. Note that the grain is essentially isopolar and in the absence of viscin threads (*C. alpina* is the only taxon in the Onagraceae without them) it is difficult, if not impossible, to determine the distal and proximal poles. E, F. Two collections of *Hauya elegans* subsp. *elegans*.—E. (*Moran 13387*). Two pollen grains in proximal polar view showing masses of viscin threads. In contrast to the pollen of *Fuchsia* (A) and *Circaea* (D) the apertural protrusions are considerably less prominent.—F. (*Rzedowski 9294*). Two groups of viscin threads exhibiting a segmented to coarsely beaded morphology. Each group consists of several individual threads aligned in parallel fashion. Attachment with the globular elements of the exine surface is partially evident in the thread group at the right.—G. *H. elegans* subsp. *barcenae*. Area of a fractured pollen grain showing thick, spongy ("paracrystalline") ektexine (ek) and solid, dense endexine (en). The short, irregular extensions at the lower margin of the ektexine are columellae (see Fig. 60C). The slightly lamellate upper margin of the endexine suggests a foot layer but it has not been confirmed in transmission electron micrograph with any degree of confidence (see Fig. 60C). The separation of ektexine from endexine is artificial, probably a result of processing. The scales equal 1 μm.

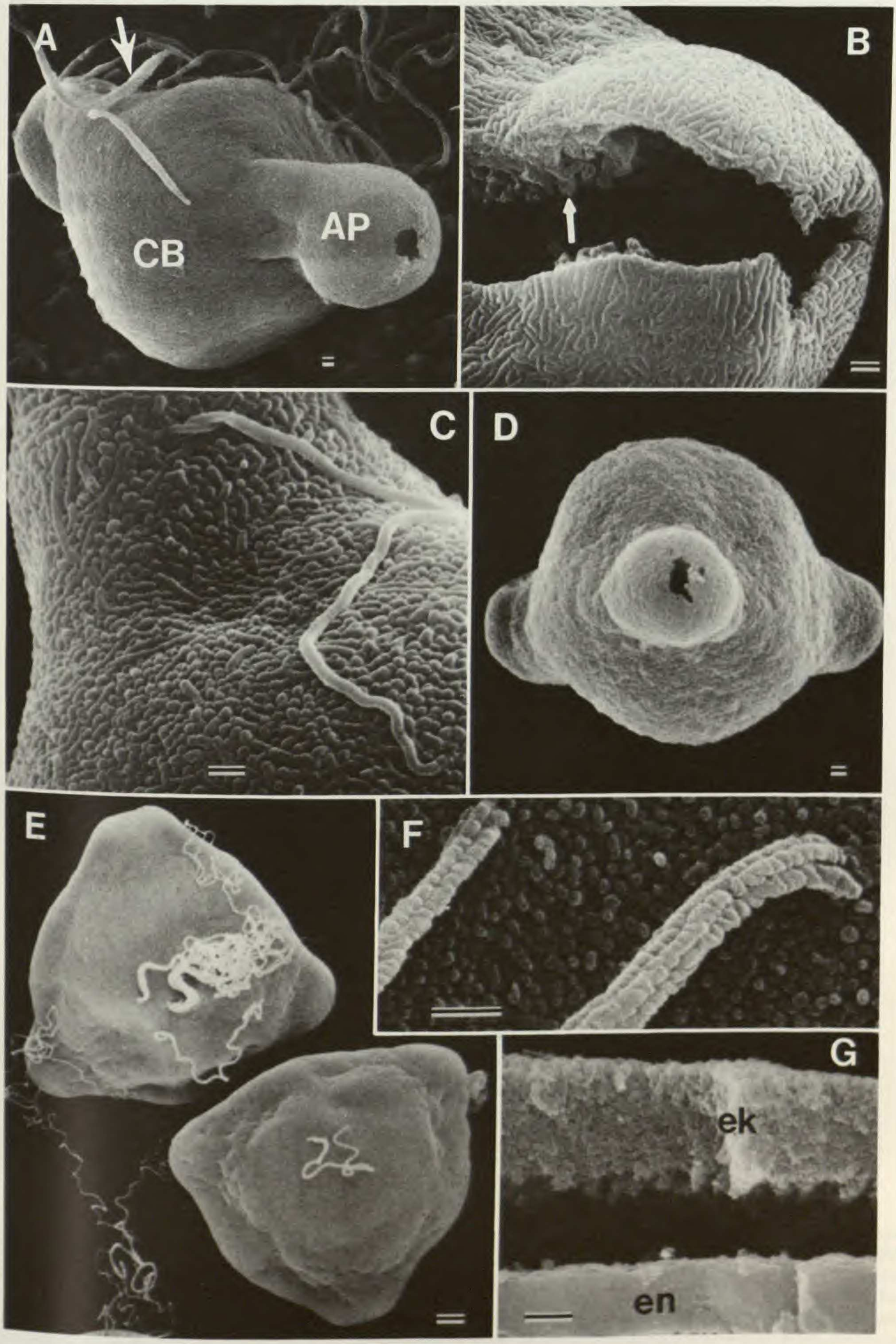
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Table 2. Summary of pollen characters in Onagraceae.[a]

	Pollen Type			Apertural Protrusions			Viscin Threads					Surface Texture				Columellae			Columellae/ Tectum			Endexine Granularity		
	M	T	P	P	NP	BCB	SM	B	R	TC	IC	G	R–E	RUG	P	P	I	A	C = T	C > T	C < T	P	NP	NE
Fuchsia	+			+					+			(+)	+	(+)				+						+
Lopezia	+					+		+				+			+	+			(+)		+			+
Circaea	+			+			+					+	+					+						
Camissonia	+	+			+		(+)		+			+				+			+			+		
Xylonagra	+				+				+			+	(+)			+					+	+		
Gongylocarpus	+					+			+			+	+				+				+		+	
Gayophytum	+					+	+		+			+	+					+						+
Hauya	+				+			+				+				+					+	+		
Calylophus	+			+				+				+	+			+			+					+
Gaura	+			+				+				+			(+)	+			+					+
Heterogaura	+			+			+					+						+						+
Clarkia	+			+			+					+	+					+						+
Oenothera	+			+				+				+	+		+		+				+			+
Stenosiphon	+			+						+		+	+			+				+				+
Ludwigia	+	+	+		+		+							+				+					+	
Boisduvalia		+				+	+			+	+			+	+		+	+	+					+
Epilobium	+	+				+				+	+		+	+	+	+	+		+	+			+	

[a] The data apply to the taxa listed in Table 1. Parentheses indicate that this observation was less common. Abbreviations for each category are:
Pollen type: M (monad), T (tetrad), P (polyad).
Apertural Protrusions: P (prominent), NP (not prominent), BCB (apertural protrusions blend into central body).
Viscin threads: SM (smooth), B (beaded), R (ropy), TC (tightly compound), IC (incised compound).
Surface texture: G (globular), R–E (rod-like to elongate), RUG (rugulate), P (porous underlying sheet).
Columellae: P (prominent), I (indistinct), A (absent).
Columellae/Tectum: $C = T$ (columellae and tectum approximately equal), $C > T$ (columellae of greater thickness than tectum), $C < T$ (tectum of greater thickness than columellae).
Endexine granularity: P (prominent), NP (not prominent), NE (not evident in this study).

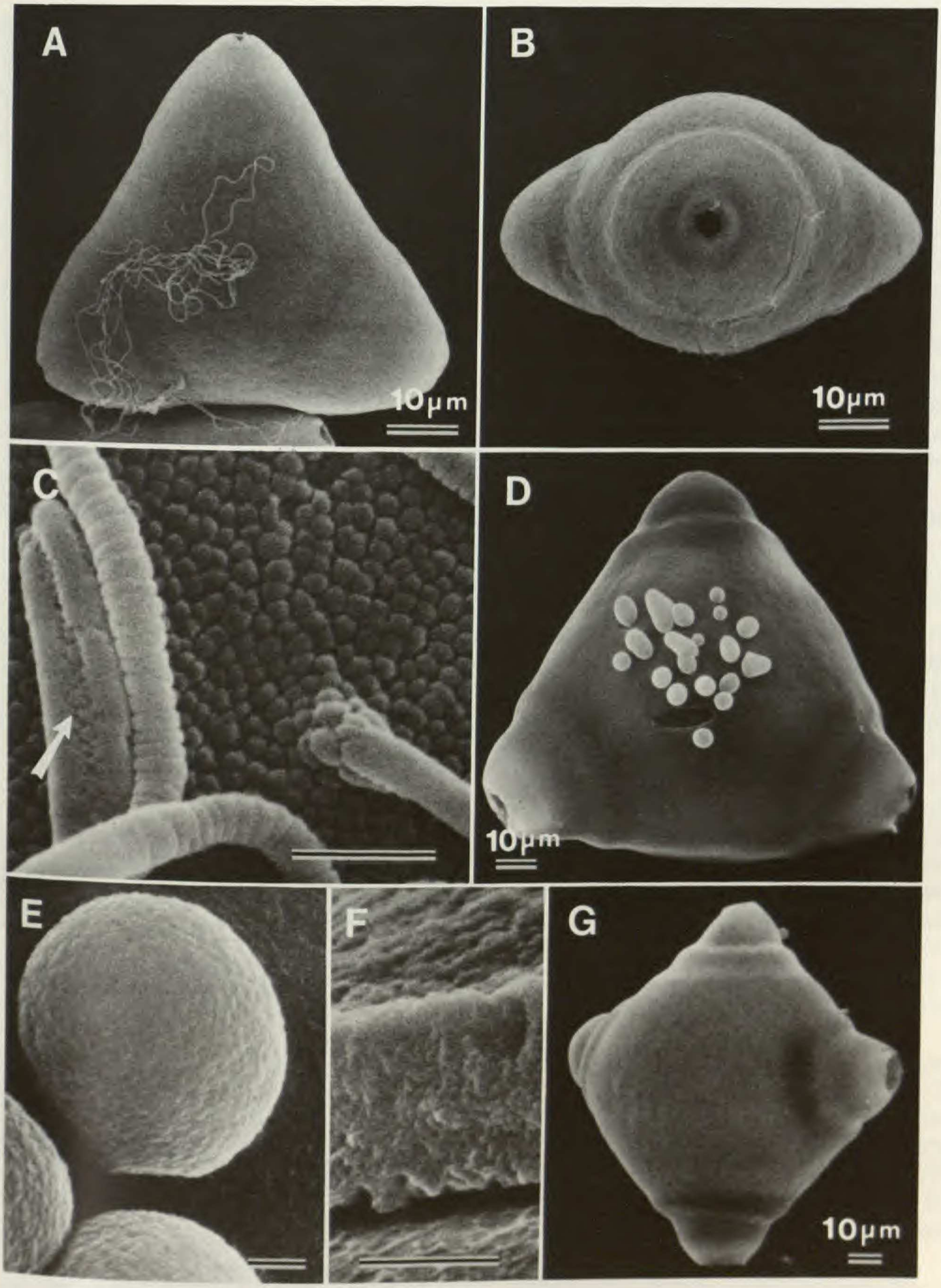
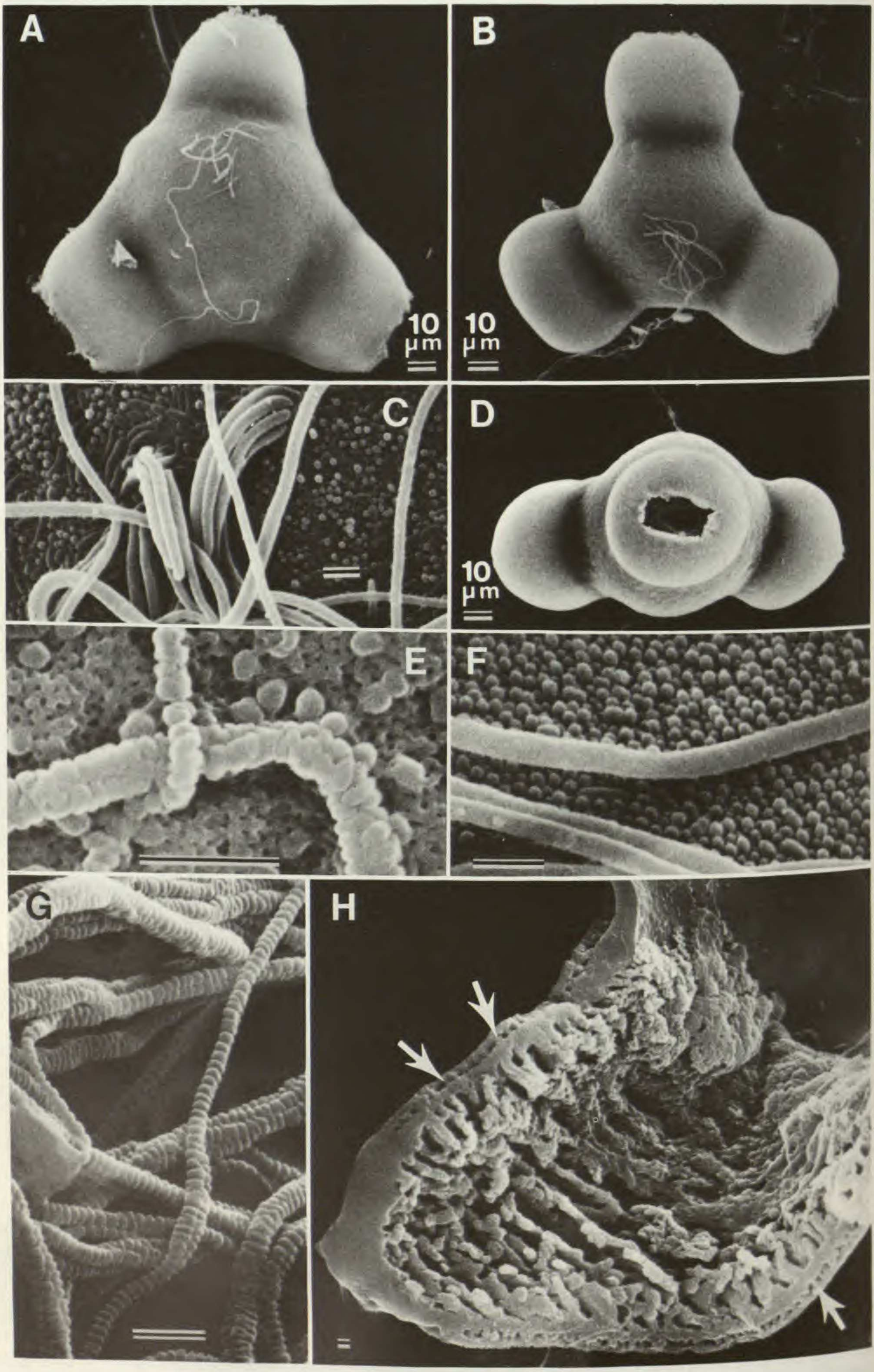


FIGURE 51. Scanning electron micrographs of Onagraceae (*Lopezia*) pollen. A–C. *L. racemosa* subsp. *racemosa*.—A. Proximal polar face with viscin threads.—B. Lateral view.—C. Surface detail showing tightly packed globular elements on a porous exine sheet. Viscin threads are beaded but some are smooth where they extend from the ektexine. Two or more threads are often united at the exine surface. Rarely a beaded-granular surface (arrow) is indicated where the two threads unite. D–G. *L. longifolia*.—D. Polar surface containing numerous globular-irregular elements, most probably Ubisch bodies. These bodies seem to be most commonly associated with pollen of *Lopezia*. Frequently, viscin threads are absent when Ubisch bodies are present.—E. Enlargement of Ubisch body. The surface of the Ubisch bodies and the exine is smooth rather than the more typically beaded appearance of *Lopezia*.—F. Fractured grain emphasizing the dense paracrystalline ektexine (cf. Fig. 50G of *Hauya*).—G. 4-aperturate pollen grain. Unless indicated otherwise, the scales equal 1 µm.


A
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strands or viscin threads on the proximal polar face (*Hauya,* Fig. 50E; *Lopezia,* Fig. 51A; *Clarkia,* Fig. 52A, B, D; *Gaura,* Fig. 53B; *Gayophytum,* Fig. 53E; *Xylonagra,* Fig. 54F; *Stenosiphon,* Fig. 55E; *Gongylocarpus,* Fig. 56D; *Camissonia,* Fig. 57C; *Epilobium,* Fig. 59B). In thin section it is clear that they are extensions of the exine surface (*Fuchsia,* Fig. 60A; *Camissonia,* Fig. 61A; *Gaura,* Fig. 62A; *Clarkia,* Fig. 62D; see also Skvarla et al., 1976).

The threads have different surface patterns: smooth (*Circaea,* Fig. 50C; *Clarkia,* Fig. 52C, F; *Gayophytum,* Fig. 53H, I; *Heterogaura,* Fig. 54C; *Boisduvalia,* Fig. 58E; and *Ludwigia,* Fig. 58F, H, I); segmented (*Hauya,* Fig. 50F; *Lopezia,* Fig. 51C; *Gaura,* Figs. 52E, G, 53C, D; *Gayophytum,* Fig. 53G; *Calylophus,* Fig. 55C; *Oenothera,* Fig. 56B, E; and *Camissonia,* Fig. 57E); tightly compound-twisted (*Stenosiphon,* Fig. 55F; *Boisduvalia,* Fig. 58C; and *Epilobium,* Fig. 59F, H, I); and incised-compound (*Epilobium,* Fig. 58B). As discussed in a more comprehensive study (Skvarla et al., 1978), some patterns are difficult to categorize and may represent intermediate or transitional forms. For example, the obliquely inclined segmented-beaded threads of *Fuchsia* (Fig. 50A), *Xylonagra* (Fig. 54D), *Gongylocarpus* (Fig. 56D), and *Camissonia* (Fig. 57E) can also be considered as segmented-ropy. Sections through viscin threads (Figs. 60E, 61G, 62E, 63G) support the morphological patterns. *Lopezia longifolia* (Fig. 51D, E) commonly has prominent spherical particles on the polar face. These particles may represent Ubisch bodies. They have been observed most frequently on *Lopezia* pollen, particularly in certain collections of *L. longifolia.* When they occur, viscin threads are usually absent.

It must be stressed that we consider the viscin threads to be an integral part of the pollen grain wall, namely, the ektexine, and have documented this relationship clearly (Skvarla et al., 1975, 1976, 1978; Praglowski et al., 1983; Nowicke et al., 1984). The phrase "attachment point(s)" was used to indicate the specific area on the exine surface where the threads emerge. The area is a simple transition from ektexine surface elements to individually protruding threads or an enlarged region with several emerging threads. We now recognize that this phrase can be misleading and might be interpreted to mean that viscin threads are not an inherent part of the exine and instead are a later addition. Viscin threads form along with other exine units, as has been shown in developmental studies dating to the early twentieth century (Beer, 1905; Bowers, 1931). In order to avoid any existing or potential confusion, perhaps "attachment point(s)" should be replaced by a more appropriate syntactic unit such as "emergence area," "extension area," etc.

While viscin threads are evident in Onagraceae and some Ericaceae (Skvarla et al., 1978), equivalent structures have also been suggested in Leguminosae (Cruden & Jensen, 1979; Graham et al., 1980). In certain species of *Caesalpinia* and *Delonix,* randomly located strands termed "exinial connections" link pollen grains, and although they are without free ends they are thought to be similar to viscin threads and to facilitate pollination (Cruden & Jensen, 1979). In pollen of *Jacqueshuberia,* the linkages are markedly longer and fewer. They are considered to be viscin threads and to indicate an adaptation to entomophily (Graham et al., 1980). Recent study (Patel et al., 1985) of *Jacqueshuberia* threads shows that the thread ends are attached to different pollen grains, therefore indicating that they are long exinial connections rather than viscin threads.

Hesse has published a series of papers (summarized in Hesse, 1981) reviewing the well-known subject of pollen cement in Angiosperm families. He contrasts "pollenkitts" and "tryphine," the sticky, viscous, lipid-carotenoid adhesive substances that are synthesized in the tapetum (i.e., by plastids or endoplasmic reticulum)

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FIGURE 52. Scanning electron micrographs of Onagraceae pollen. A, C. *Clarkia speciosa* subsp. *speciosa.*—A. Proximal polar view with several viscin threads extending from the exine surface.—C. View showing smooth viscin threads. Although not clearly indicated, the exine surface is composed of distinct globular and elongate elements. B, D, F. *C. unguiculata.*—B. Proximal polar view.—D. Lateral view with viscin threads in association with proximal (top) pole (compare with *C. alpina* subsp. *imaicola,* Fig. 50D).—F. View showing globular elements of exine surface and smooth viscin threads.—E. *Gaura lindheimeri.* The viscin threads are segmented-coarsely beaded. The exine surface has randomly dispersed globular elements on a perforate surface. G, H. *G. mutabilis.*—G. Segmented-beaded viscin threads.—H. Fractured apertural protrusion showing short columellae (arrows) and rows of lamellar endexine within the protrusion. Unless indicated otherwise, the scales equal 1 μm.

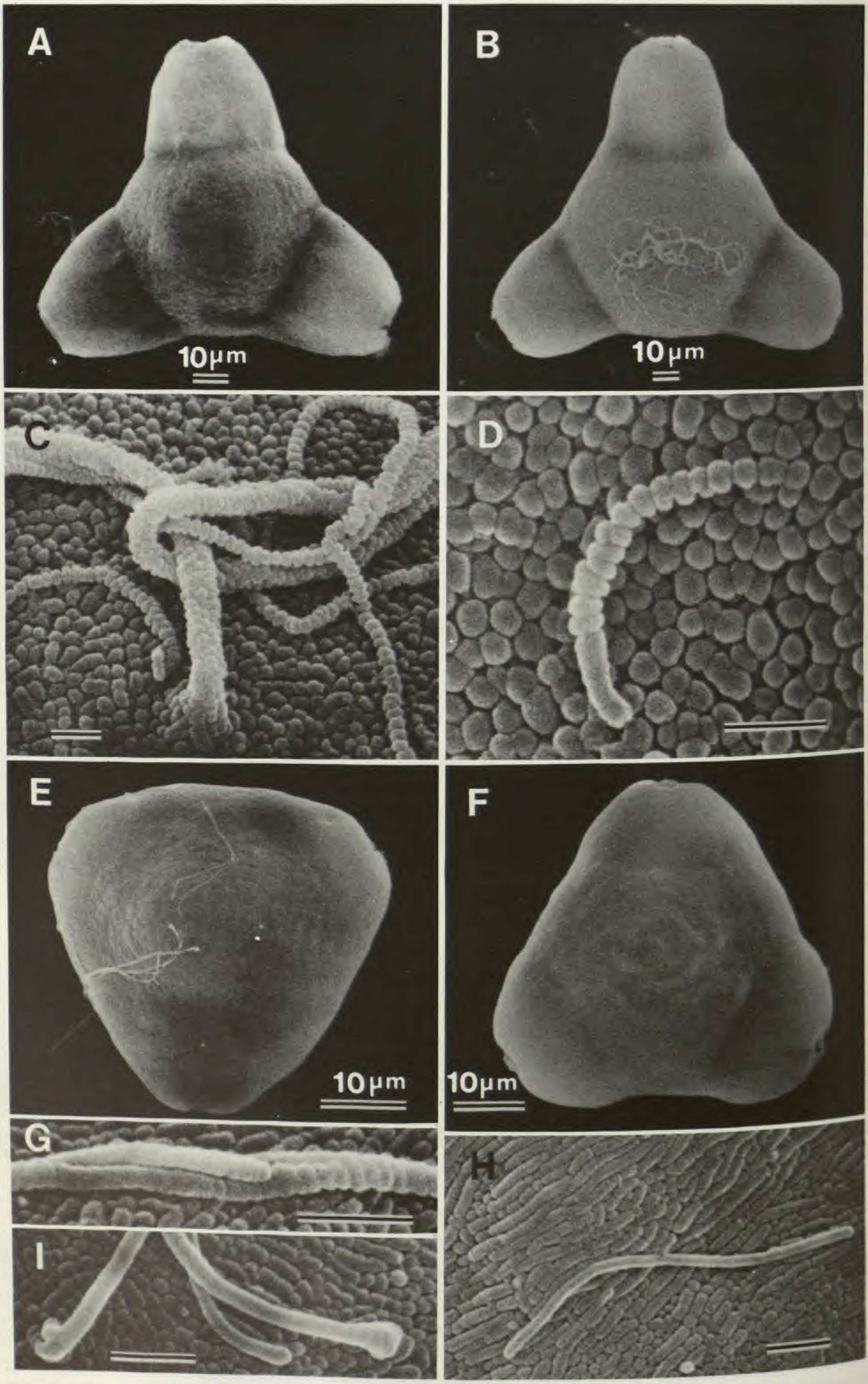


FIGURE 53. Scanning electron micrographs of Onagraceae pollen.—A. *Gaura calcicola.* Distal polar view emphasizing prominent apertural protrusions. B, C. *G. neomexicana.*—B. Proximal polar view with viscin threads.—C. Beaded viscin threads and exine.—D. *G. demareei.* This beaded viscin thread originates from the apertural protrusions, rather than the proximal polar face. Viscin threads in the area of the apertures have been documented previously for *Lopezia* (Skvarla et al., 1978) and possibly for S_3S_4 genotype grains of *Oenother*

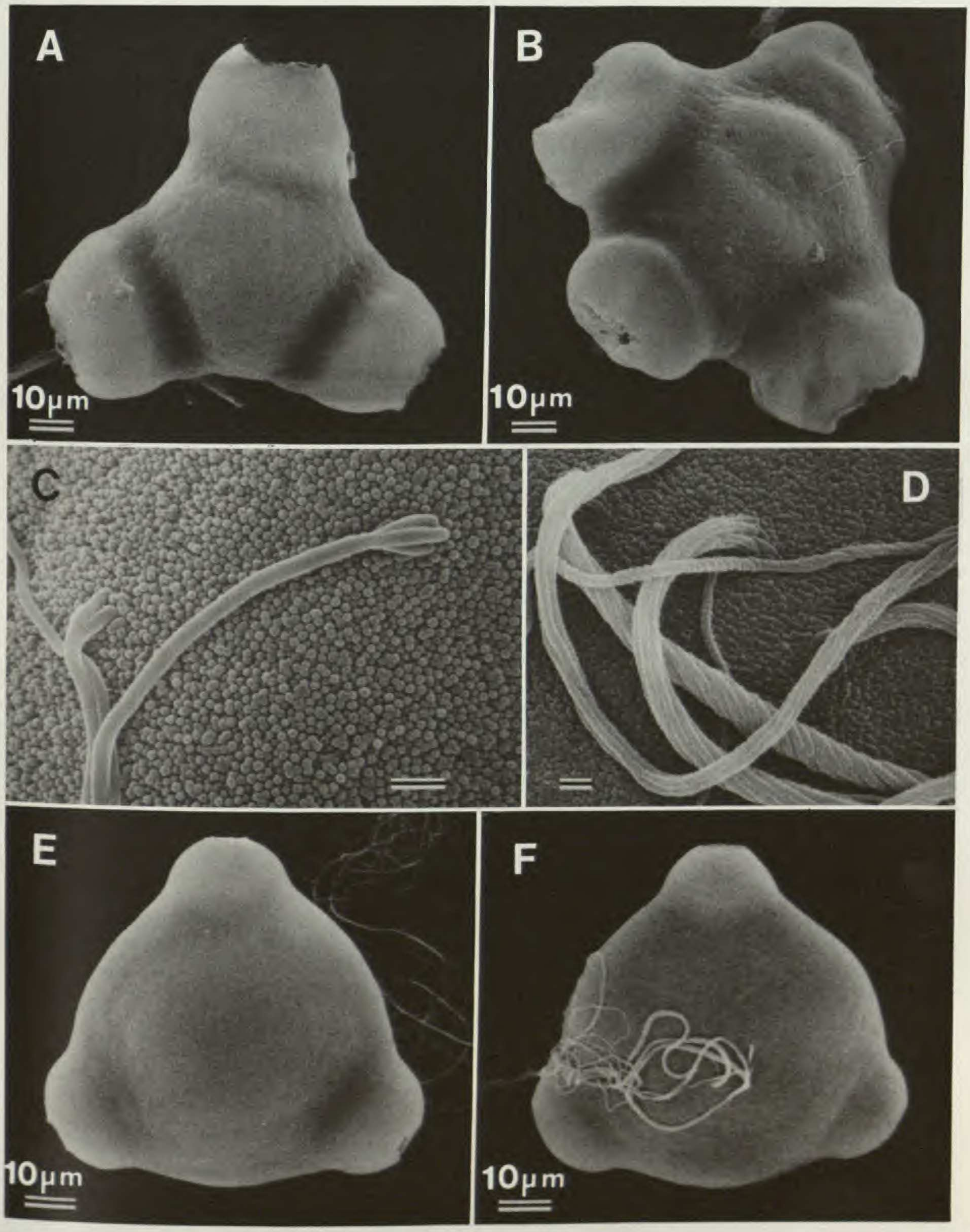


FIGURE 54. Scanning electron micrographs of Onagraceae pollen. A–C. *Heterogaura heterandra.*—A. Distal polar view.—B. 4-aperturate pollen grain in proximal polar view.—C. Smooth viscin threads with forked bases and a highly globular exine surface typically characterize the proximal face. D–F. *Xylonagra arborea* subsp. *wigginsii.*—D. Groups of twisted (segmented-ropy) viscin threads.—E. Distal polar face.—F. Proximal polar surface. Unless noted otherwise, the scales equal 1 μm.

←

organensis (Cresti et al., 1983). E, G, I. *Gayophytum ramosissimum.*—E. Proximal polar view.—G. A portion of a branched viscin thread. In comparison with other areas of this thread which are smooth (not illustrated here), this area is segmented-twisted (ropy).—I. Three viscin threads (see E) extending from an exine surface composed of globular-elongate elements arranged in a striate pattern that is characteristic of this genus. Note that one of the smooth threads appears lightly segmented-twisted (ropy) only at the point of attachment. F, H. *Gayophytum micranthum.*—F. Distal polar view.—H. A smooth, short viscin thread on a markedly striate exine surface of globular-elongate elements. Numerous short threads, some appearing as partially sloughed off exine surface elements or striae (not illustrated here) also have been noted along with normal threads. Unpublished data suggest that *G. micranthum* may also possess segmented-twisted threads (as shown for *G. ramosissimum*). Unless indicated otherwise, the scale equals 1 μm.

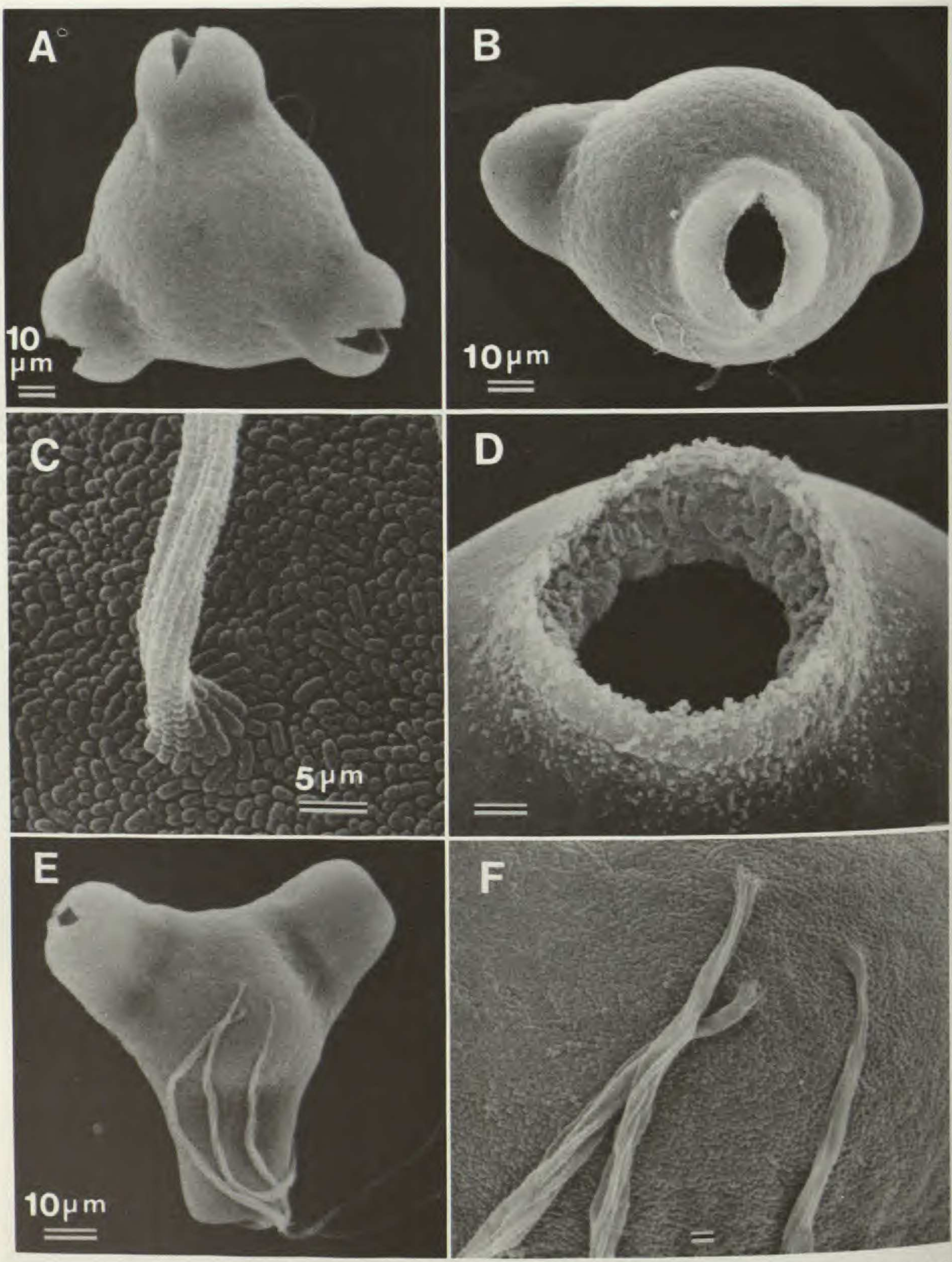
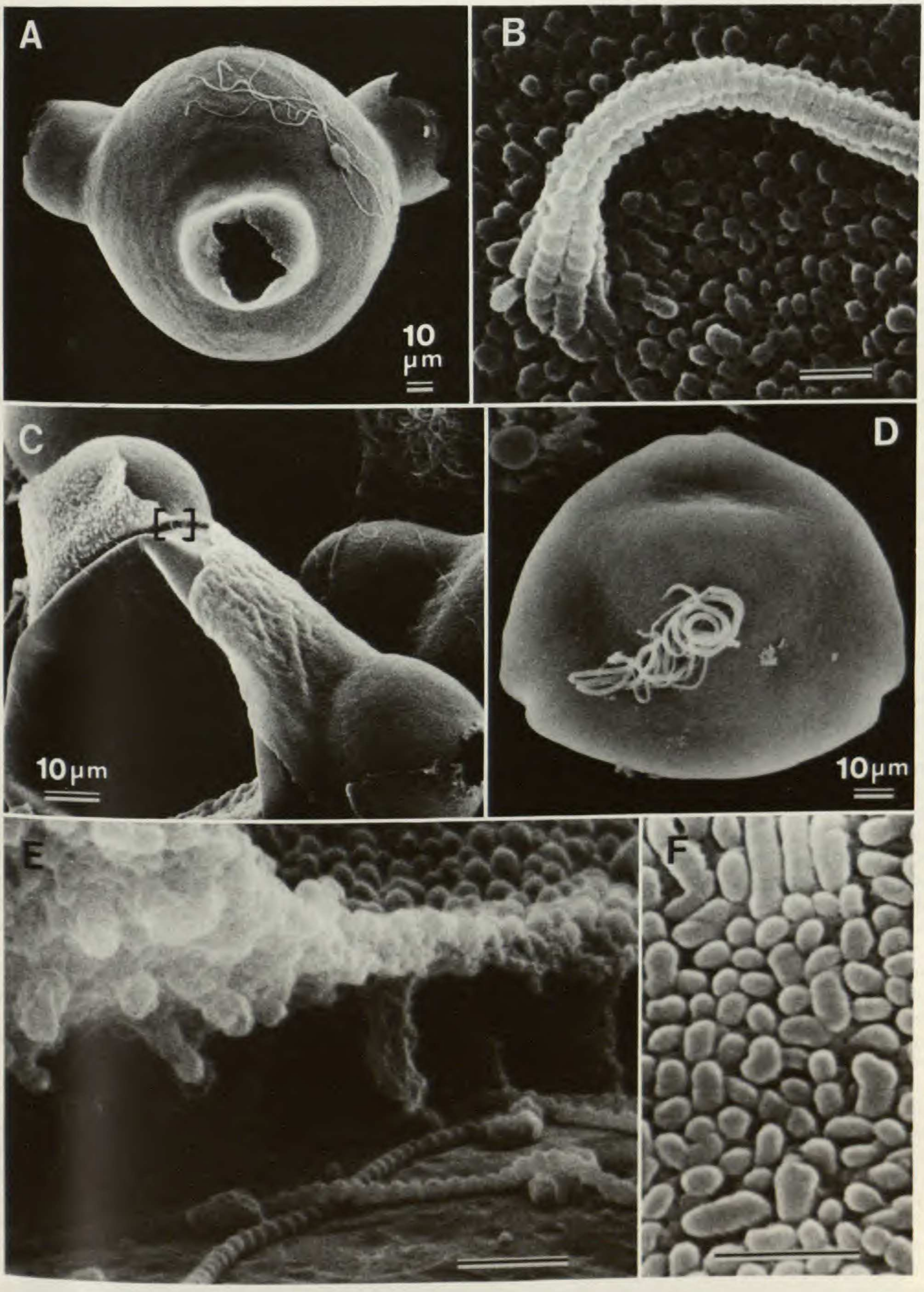


FIGURE 55. Scanning electron micrographs of Onagraceae pollen. A–D. *Calylophus toumeyi.*—A. Distal polar view.—B. Lateral view.—C. A group of beaded viscin threads extends from a surface which consists of globular-elongate elements.—D. Pore region showing internal construction of irregular sporopollenin. The ektexine has been peeled away leaving broken columellae on the endexine. Within the pore is lamellar endexine. E, F. *Stenosiphon linifolius.*—E. Proximal polar view with three groups of viscin threads.—F. Enlarged view of E showing smooth-twisted (tightly compound) viscin threads on a globular to rod-like polar surface. Unless indicated otherwise, the scales equal 1 µm.

FIGURE 56. Scanning electron micrographs of Onagraceae. A, B. *Oenothera brachycarpa.*—A. Lateral view similar to *Circaea alpina* subsp. *imaicola* (Fig. 50D) and *Clarkia unguiculata* (Fig. 52D).—B. A group of segmented-beaded viscin threads extends from a perforate exine surface composed of globular-elongate elements. C, E. *O. texensis.*—C. The pollen grain is collapsed as well as fractured. The apertural protrusion at the top is



mostly covered by exine material that has folded back to expose the columellae which appear as white dots. Randomly arranged viscin threads are intermingled with the columellae as well as with the exposed endexine surface, an artificial association resulting from collapse and fracture of the exine. The bracketed area appears in E.—E. Bracketed area of C emphasizing prominent spongy-perforate columellae and narrow tectum (compare with *H. elegans* subsp. *barcenae,* Fig. 50G). Several segmented-beaded viscin threads are on the surface of the endexine.—D. *Gongylocarpus rubricaulis* (*Sharp 44846*). Proximal polar view showing mass of viscin threads. In contrast to other Onagraceae taxa, apertural protrusions are considerably less conspicuous.—F. *G. fruticulosus* subsp. *glaber.* View of exine composed of short rod-like and globular elements of variable sizes. Unless indicated otherwise, the scales equal 1 µm.

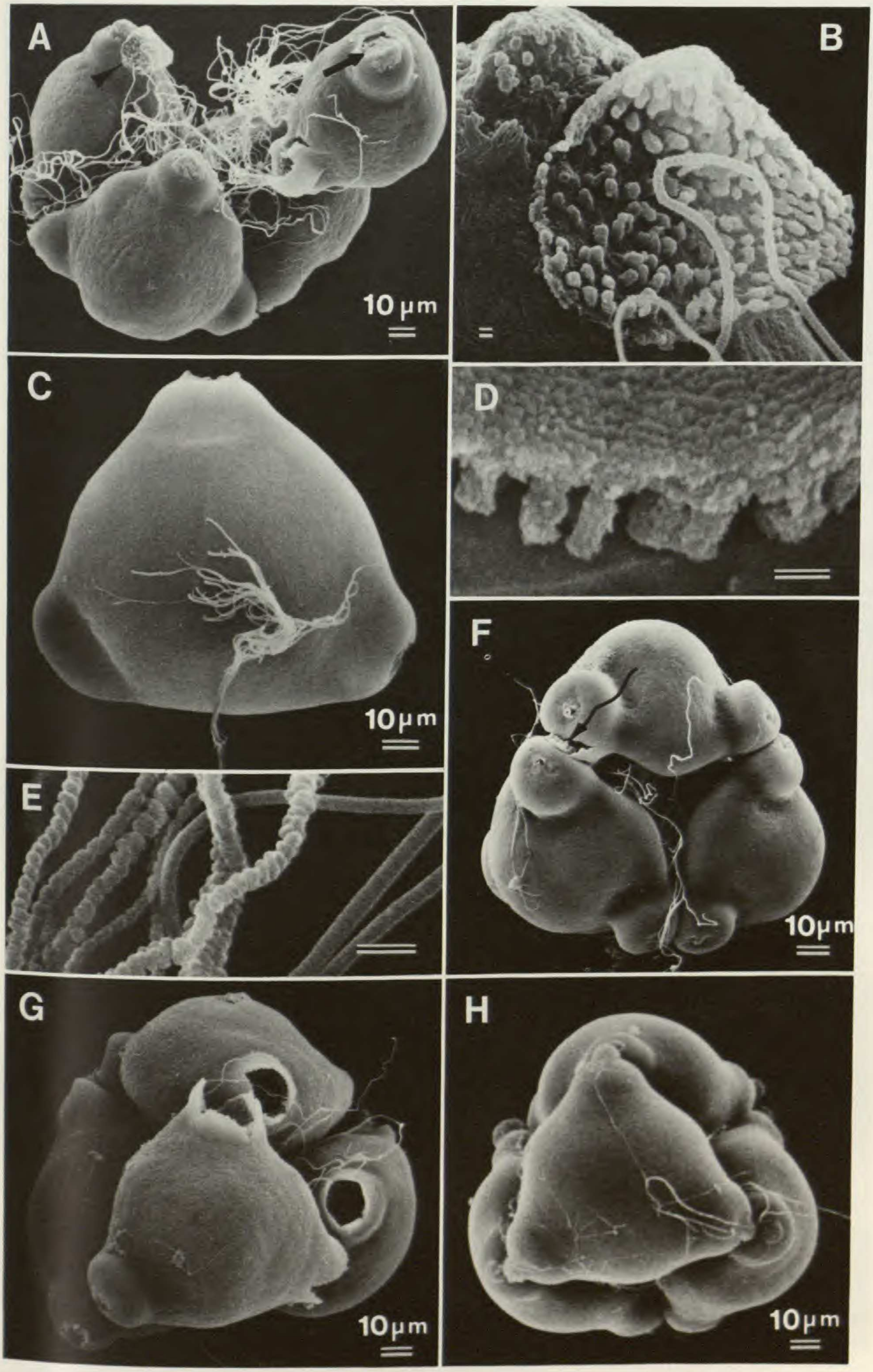
or as tapetal breakdown products (Dickinson, 1973; Dickinson & Lewis, 1973), with viscin threads, which he considers to be non-sticky, non-viscous, and non-tapetally derived. He regards their development as beginning in a granular matrix of the anther loculus at the same time that an ektexine is developing on matrix-encased microspores. Hesse (1981) shows transmission electron micrographs in which he states that the threads approach the ektexine when it is almost completely formed and fuse with the surface. He further postulates that the viscin threads arose as a chance mutation.

Sculpturing of the exine surface is also variable throughout the family and is illustrated by globular elements (*Hauya,* Fig. 50F; *Lopezia,* Fig. 51C; *Clarkia,* Fig. 52F; *Gaura,* Figs. 52E, 53C, D; *Heterogaura,* Fig. 54C; *Xylonagra,* Fig. 54D;

FIGURE 57. Scanning electron micrographs of Onagraceae (*Camissonia*) pollen. A, B, D, F. *C. arenaria.*—A. Tetrad (unacetolyzed) which is partially disrupted at two apertures. The arrowhead designates the aperture containing the exine fragment (i.e., "spur" of Skvarla et al., 1975) torn from the corresponding aperture designated by an arrow.—B. Enlargement of spur in A. The abundant short structures are the columellae which line the aperture protrusion. Also evident is a beaded viscin thread.—D. Fractured grain (acetolyzed) showing columellae structure at the junction of the central body and apertural protrusion.—F. Acetolyzed tetrad. The arrow indicates a partial disruption in one aperture region.—C. *C. tanacetifolia* subsp. *tanacetifolia.* Monad pollen grain. Numerous viscin threads extend from different areas of the proximal polar face. E, G. *C. cardiophylla* subsp. *robusta.*—E. The viscin threads are primarily beaded-ropy but a few are also smooth (see Skvarla et al., 1978).—G. Intact tetrad (acetolyzed).—H. *C. cardiophylla* subsp. *cardiophylla.* Intact tetrad (unacetolyzed). Unless indicated otherwise, the scales equal 1 μm.

FIGURE 58. Scanning electron micrographs of Onagraceae pollen.—A. *Boisduvalia stricta.* View of tetrahedral tetrad showing all four pollen members. B, C, E.—*B. densiflora.* These three scanning electron micrographs represent different collections and illustrate the diversity in viscin thread morphology which occurs on pollen in some Onagraceae taxa. In B (*Piper s.n.*), the morphology is clearly incised-compound, in C (*Thompson 5099*), it appears as tightly compound-twisted, and in E (*Piper s.n.*), it is smooth (see Skvarla et al., 1978 for detailed discussion). In all three examples, the associated exine surface appears to be rugulate-perforate. D, G. *Ludwigia goiasensis.*—D. The tetrad (fourth pollen member is not visible) is part of a polyad and is surrounded by parts of other tetrads. The bracketed area is enlarged below in G. Arrowheads indicate colpi.—G. Enlargement of bracketed area in D showing internal bridges (arrows) between adjacent pollen grains of the tetrad. The nature of the globular club-like structure associated with one of the bridges is unknown but may be related to viscin threads. The star represents union of adjacent pollen grain apertures.—F. *L. alternifolia.* Three members of a tetrad. The large open arrows indicate prominent meridional ridges characteristic of several *Ludwigia* species and which bifurcate at the equator to join with the equatorial ridges between the apertural protrusions. In contrast to *L. goiasensis* (D) and *L. longifolia* (H) the meridional ridges are best developed in *L. alternifolia* while the equatorial ridges are of equal prominence in all three species. The short, solid arrows show the colpi. H, I. *L. longifolia.*—H. Overall view of a polyad with basic tetrad composition. Arrow indicates an external bridge which connects adjacent distal tetrad pollen surfaces and maintains polyad unity. Arrowheads indicate colpi.—I. External bridge (not from H) with portions of adjacent exine surfaces and smooth viscin threads. Unless indicated otherwise, the scales equal 1 μm.

FIGURE 59. Scanning electron micrographs of Onagraceae (*Epilobium*) pollen. A–D. *E. brachycarpum.*—A. In distal polar view the pollen outline is nearly circular. The surface is composed of numerous randomly arranged short rod-like elements.—B. Viscin threads (smooth and incised compound, see Skvarla et al., 1978) originate from the center of the proximal polar surface. The sculpturing at the proximal pole shows thin-elongated elements. The surface becomes more coarse toward the equator and consists of rod-like or rugulate elements (see also Skvarla et al., 1978, Pl. 45). The remainder of the proximal polar face is also composed of rod-like or rugulate elements but they are not densely organized.—C. Enlarged view of exine surface showing that the rod-like or rugulate elements are underlain by a highly porous layer or sheet.—D. Fractured exine showing a channeled endexine (indicated by a bracket) and a "columellae" layer composed of randomly arranged porous sheets (arrows) which appear to be vertically oriented. The tectum is a continuous porous sheet (see C) upon which rod-like or rugulate elements are scattered. E–G. *E. brachycarpum.* This collection documents the rare occurrence of tetrads.—E. A tetrad.—F. Smooth and incised compound viscin threads occur on a surface similar to Figure 50B.—G. View of fractured exine surface. The arrows indicate the porous sheets as described above (see D).—H. *E. glaberrimum.* This view documents the only observation of a viscin thread (tightly compound) originating from an exine bridge connecting adjacent members of a tetrad.—I. *E. rigidum.* Numerous exine bridges show the same morphology (tightly compound) as the viscin thread at the left margin (see also Skvarla et al., 1978, Pl. 48).—J. *E. hectorii.* In this view exine bridges between adjacent tetrad members are clearly illustrated (arrows). Unless designated otherwise, the scales equal 1 μm.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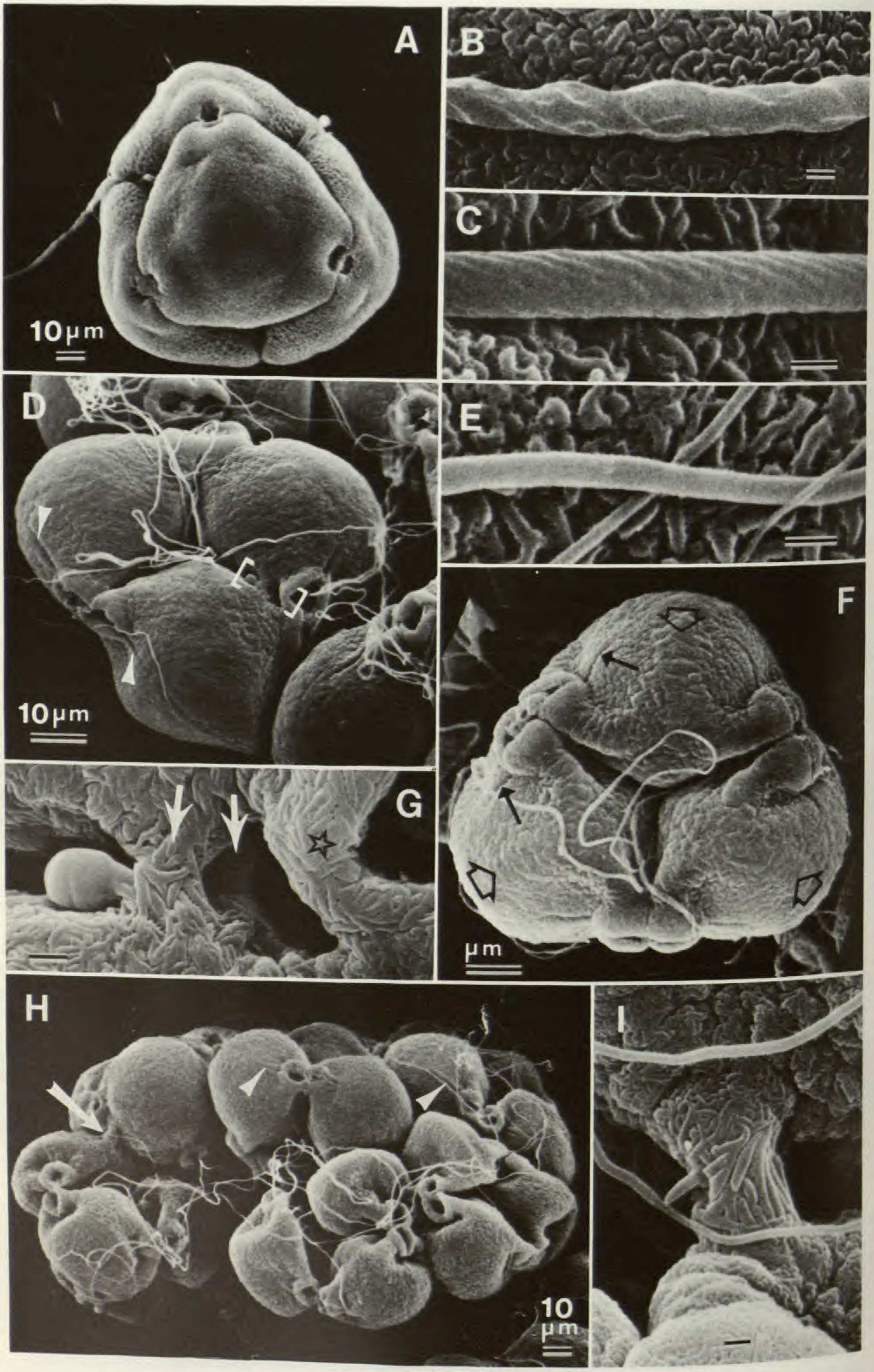
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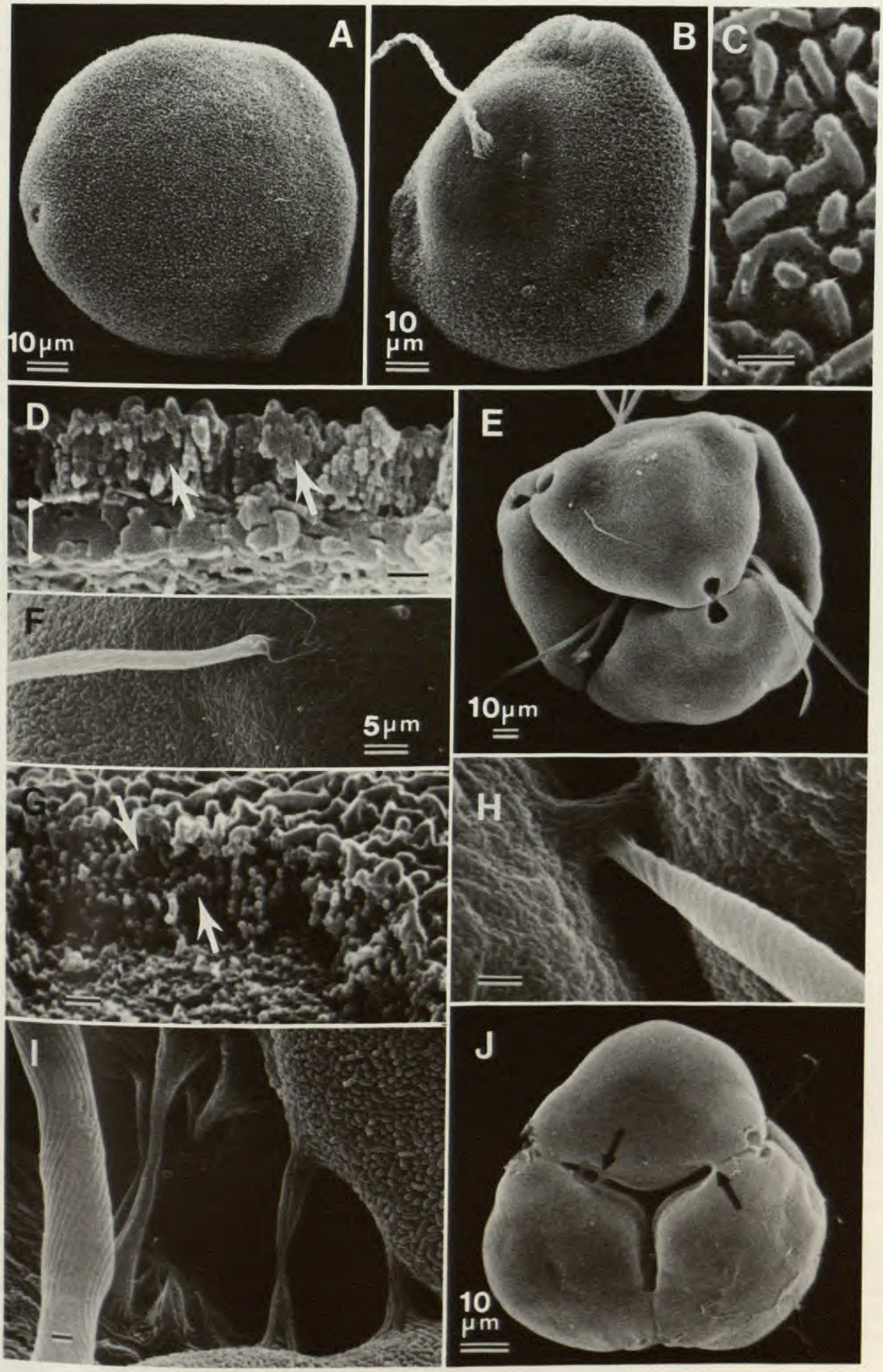
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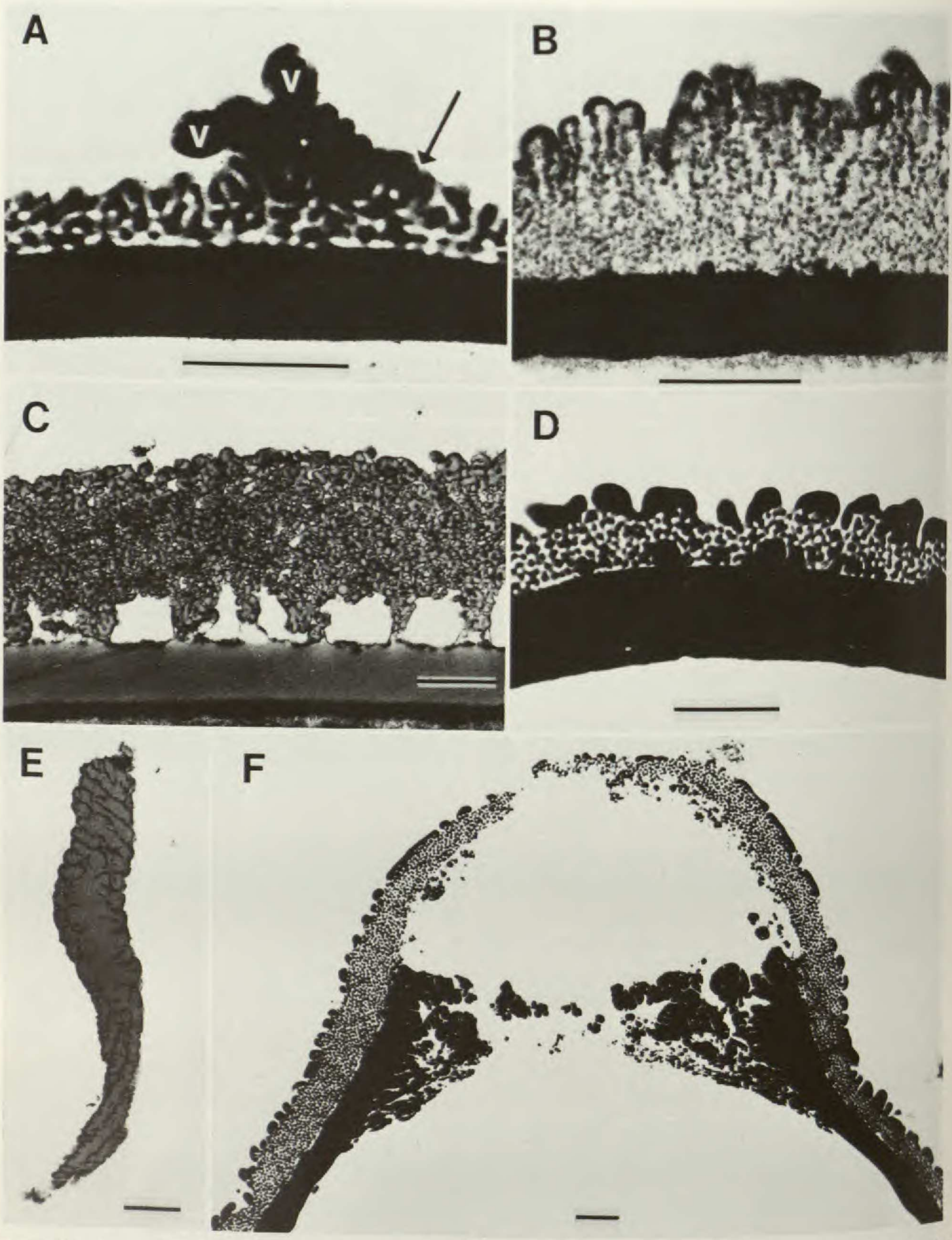

FIGURE 60. Transmission electron micrographs of Onagraceae pollen.—A. *Fuchsia garleppiana.* Section at proximal pole showing irregular and coarse spongy-paracrystalline ektexine attached (without columellae) to the uniform and solid endexine. The arrow indicates extension of viscin threads (v) from the ektexine.—B. *Ludwigia brevipes.* Section is through the distal face. The ektexine is massive and spongy-paracrystalline and the surface is markedly undulate. The endexine is uniform and solid and has a thin granular basal area. C, E. *Hauya heydeana.*—C. This sample represents fresh pollen prepared in glutaraldehyde and osmium tetroxide (acetolysis has been omitted). It is very similar to the fractured grain of *Hauya elegans* subsp. *barcenae* (Fig. 50G) but clearly emphasizes the short but prominent columellae. Although not clearly distinguished because of the cytoplasm, the endexine has a granular basal component.—E. Section through a group of viscin threads showing serrated margins indicative of a segmented morphology (see Skvarla et al., 1978, Pl. 20, 21). D, F. *Circaea mollis.*—D. The surface elements on the highly undulate exine surface appear as irregularly shaped isolated islands in sectional view. Also note that the upper surface of the endexine is irregular and appears to "outpocket" into the ektexine network.—F. Section through apertural protrusion showing apertural chamber underlain by a thickened zone of lamellar endexine. Scales equal 1 μm.

and *Camissonia,* Fig. 57D); rod-like or elongate elements (*Fuchsia,* Fig. 50B; *Boisduvalia,* Fig. 59C); rugulate or coarsely elongate elements (*Fuchsia,* Fig. 50B; *Boisduvalia,* Fig. 58B, C, E; *Ludwigia,* Fig. 58F, G, I; *Epilobium,* Fig. 59G); and combinations of globular and rod-like elongate elements (*Circaea,* Fig. 50C; *Clarkia,* Fig. 52C; *Gayophytum,* Fig. 53H, I; *Calylophus,* Fig. 55C; *Stenosiphon,* Fig. 55F; *Oenothera,* Fig. 56B; *Gongylocarpus,* Fig. 56F; and *Epilobium,* Fig. 59I). As discussed for viscin threads, some of the patterns are difficult to precisely categorize and therefore are amenable to considerable subjectivity. For example, slightly enlarged globular elements could be interpreted as rod-like to elongate, and extension of the latter could be interpreted as rugulate. Obviously, it is more important to be cognizant of these differences rather than being overly concerned with their exact categorization. Similarly, there should be no conflict when other descriptive terms—granular for globular and vermiculate for elongate and rugulate—are employed (Daghlian et al., 1984). Frequently, the surface elements are underlain by a highly perforate sheet or layer (*Lopezia,* Fig. 51C; *Gaura lindheimeri,* Fig. 52E; *Oenothera,* Fig. 56B; *Boisduvalia,* Fig. 58B, C, E; *Epilobium,* Fig. 59C).

Other surface features of significance are the long colpi and prominent ridges in *Ludwigia* (Fig. 58D, F, H). The latter are of two types: meridional ridges, which occur over the polar faces and extend to the "equator" in the area midway between the apertural protrusions, and lateral ridges, which occur between the apertural protrusions and are joined with the meridional ridges (*L. alternifolia,* Fig. 58F). Of the two, the lateral ridges seem to be the most consistent. In contrast, the meridional ridges are prominent in *L. alternifolia* (Fig. 58F) but poorly developed in *L. goiasensis* (Fig. 58D) and *L. longifolia* (Fig. 58H). Long colpi also were noted in *Calylophus* (Fig. 55A), although of less prominence than in *Ludwigia.*

Exine structure as observed in TEM as well as in fractured grains in SEM (Figs. 50G, 51F, 56E, F, 57B, D, 59D, G) indicates that it is composed of a network of spongy-paracrystalline ektexine and a dense, uniform endexine that frequently has a thin, granular, basal component (*Ludwigia,* Fig. 60B; *Camissonia,* Fig. 61A; *Xylonagra,* Fig. 61C; *Gongylocarpus,* Fig. 61H; *Epilobium,* Fig. 63D), and less frequently an irregular upper surface (Figs. 60B, D, F, 62D, 63E). The ektexine is without a foot layer and the columellae and tectum units are not always clearly recognized. Several ektexine structural patterns are evident. In *Hauya* (Fig. 60C), *Camissonia* (Fig. 61A), *Lopezia* (Fig. 61B), *Xylonagra* (Fig. 61C), *Calylophus* (Fig. 61E), *Gaura* (Fig. 62A), *Stenosiphon* (Fig. 62F), and *Epilobium cylindricum* (Fig. 63F), columellae and tectum are evident. In *Fuchsia* (Fig. 60A), *Ludwigia* (Fig. 60B), *Circaea* (Fig. 60D), *Gayophytum* (Fig. 61D), *Heterogaura* (Fig. 62C), *Clarkia* (Fig. 62D), and *Boisduvalia marantha* (Fig. 63A, B), columellae and tectum are absent and the ektexine is composed of the spongy-paracrystalline-beaded sporopollenin network. In fractured exines of *E. brachycarpum* (Fig. 59D, G), this network appears to consist of porous sheets. *Clarkia* (Fig. 62D) is further distinguished by a partial separation of ektexine from endexine and their subsequent union in the apertural protrusions. In *Gongylocarpus* (Fig. 61H), *Oenothera* (Fig. 62E), *Boisduvalia densiflora* (Fig. 63C), *Epilobium hirsutum* (Fig. 63E) and *E. collinum* (Fig. 63G) extremely short columellae are present, although this is a highly subjective interpretation and it may be more accurate to regard this group as transitional. It is clear that Onagraceae pollen does not possess typical columellae, if indeed any columellae at all, and it might be more useful to consider the ektexine to be without them. This lack of columellae, coupled with the absence of a tectum and foot layer, leads to an interpretation of the Onagraceae ektexine as being without the tripartite units that characterize Angiosperm exines.

Also subject to redefinition is the layer we regard as endexine. Whereas in previous studies we defined as endexine the dense, massive layer underlying the spongy-paracrystalline ektexine, we now might redefine it as the foot layer to the ektexine. Support for this interpretation can be found in the aperture protrusions, where the so-called endexine has the spongy-paracrystalline appearance of the ektexine (Figs. 60F, 61F, 62B), and indeed is continuous with it (see also Skvarla et al., 1976; Nowicke et al., 1984). By this interpretation the narrow, granular layer that was regarded as a basal endexine component is now the endexine. The endexine in Onagraceae pollen would be defined then as extremely narrow, sporadic, and best developed in the apertures where coarse granules are evident (Nowicke et al., 1984). We do not necessarily support this explanation, but discuss it as an illustration of the complexity and multiplicity of interpretations amenable for Onagraceae pollen.

It is apparent from observation of the exine sections in Figures 60–63 that there are differences in the texture of ektexine sporopollenin network. *Fuchsia* (Fig. 60A) has a coarse, irregularly shaped network while *Clarkia* (Fig. 62D) has a considerably finer network, and in *Boisduvalia* (Fig. 60A, B) the network appears to consist of finely connected beads and porous sheets. This has yet to be critically analyzed. Perhaps this type of study, in conjunction with analysis of ektexine "porosity," would be of value in distinguishing the various taxa.

In the apertural protrusions, the apertural chamber is usually overlain by spongy ektexine and underlain by thick layers of endexine lamellae (*Circaea,* Fig. 60F; *Calylophus,* Fig. 61F). The lamellae usually have fine channels and a spongy-paracrystalline composition similar to the ektexine. In *Gaura* (Fig. 62B), the apertural chamber is remarkable in that lamellae line the entire chamber. Grains fractured through the apertural protrusions also clearly show these endexine lamellae (*Fuchsia,* Fig. 50B; *Gaura,* Fig. 52H; *Calylophus,* Fig. 55D).

Table 2 summarizes some of the pollen wall characters of Onagraceae discussed above.

Discussion

Onagraceae pollen has been the object of studies using light (Mitroiu, 1961–1962; Ting, 1966; Brown, 1967) and electron microscopy (Skvarla et al., 1975, 1976, 1978). These studies have shown that the pollen of the 17 genera and approximately 650 species possess the following distinctive features: viscin threads, a spongy-paracrystalline ektexine, apertural protrusions, and a large central body; tetrads and/or polyads

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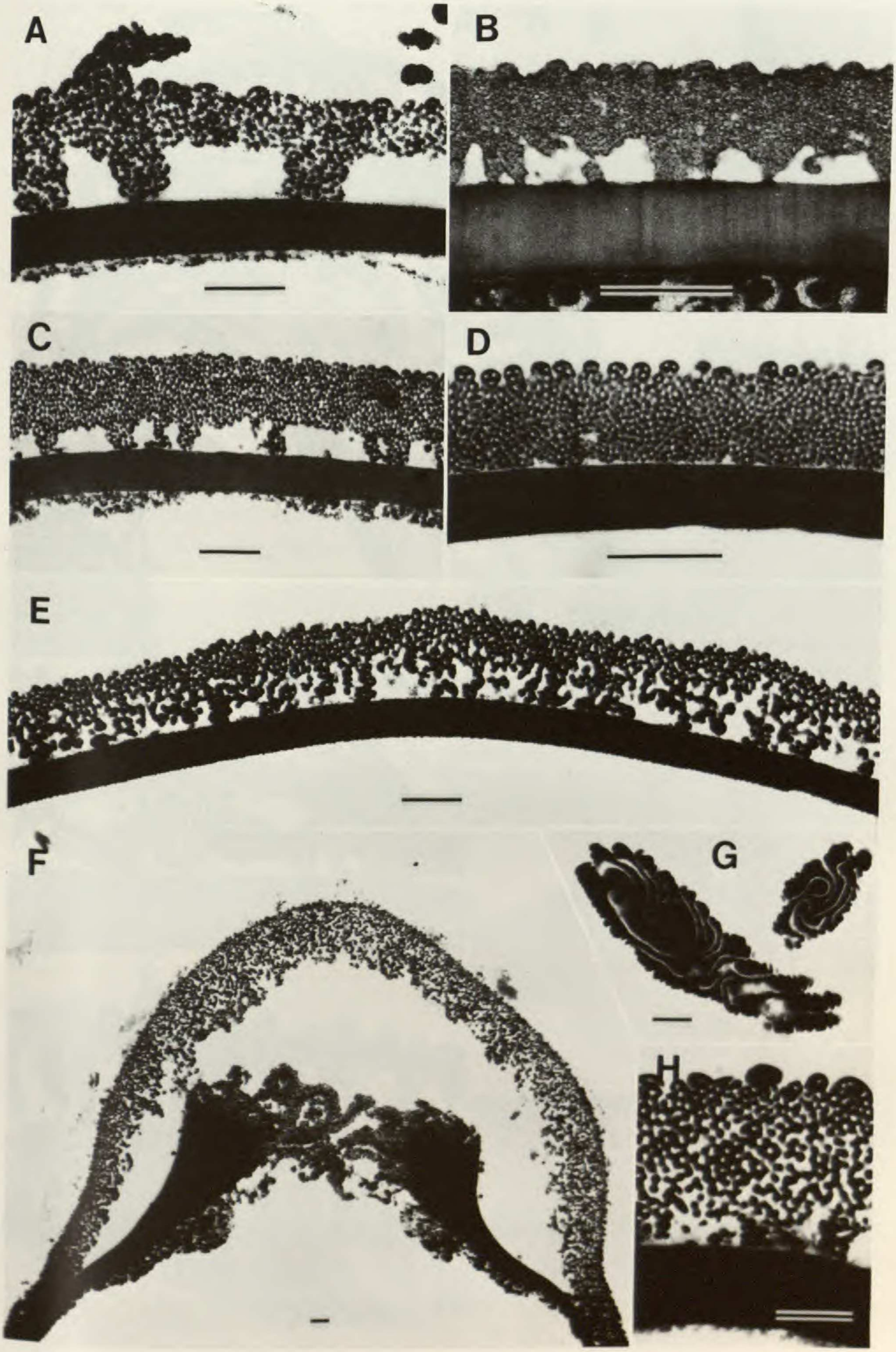
FIGURE 61. Transmission electron micrographs of Onagraceae pollen.—A. *Camissonia arenaria.* View at proximal face showing origin of viscin thread from the ektexine surface. Paracrystalline columellae are broad and nearly as thick as the overlying paracrystalline tectum. The lower margin of the endexine is composed of an irregular granular sheet.—B. *Lopezia grandiflora.* Fresh (unacetolyzed) pollen. Columellae are less pronounced than in *C. arenaria.*—C. *Xylonagra arborea* subsp. *wigginsii.* View at center of either the polar or lateral face. Pollen of this taxon is typically characterized by an irregular granular component at the lower portion of the endexine.—D. *Gayophytum micranthum.* View at center of distal polar face. Columellae are absent and the ektexine is in direct contact with the endexine. E, F. *Calylophus berlandieri* subsp. *berlandieri.*—E. Section through center of either lateral or polar face. Columellae development is somewhat intermediate between *Lopezia* (B) and *Camissonia* (A).—F. Section through aperture chamber. Note similarity to *Circaea* (Fig. 60F) and dissimilarity to *Gaura* (Fig. 62B). G, H. *Gongylocarpus rubricaulis* (*Davidse 9790*).—G. Section through two viscin threads showing the segmented-ropy morphology.—H. Columellae are only slightly developed. Scales equal 1 μm.

FIGURE 62. Transmission electron micrographs of Onagraceae pollen. A, B. *Gaura coccinea.*—A. Section at proximal face. Note short columellae and viscin thread origin from the ektexine.—B. Section through apertural protrusion. Note close similarity to fractured apertural protrusion of *Gaura mutabilis* (Fig. 52H).—C. *Heterogaura heterandra.* Fresh pollen. Columellae are absent (cf. *Gayophytum micranthum,* Fig. 61D).—D. *Clarkia breweri.* Section at proximal face. The ektexine is characteristically without columellae and separated from the endexine (see Skvarla et al., 1976, Pl. 2F). Two groups of viscin thread are evident. The upper ektexine surface suggests a faint "outpocketing."—E. *Oenothera maysillesii.* Section at proximal face showing markedly undulate ektexine, virtually indistinguishable columellae and viscin thread extension of the ektexine.—F. *Stenosiphon virgatus.* Section through center of either the polar or lateral face. Long, slender columellae are prominent. Scales equal 1 μm.

FIGURE 63. Transmission electron micrographs of Onagraceae pollen. A, B. *Boisduvalia macrantha.*—A. Section includes the flank of one apertural protrusion as well as an oblique view of an attached aperture margin of a second pollen grain. The ektexine is composed of thin, beaded, porous elements (see Skvarla et al., 1976, Pl. 8D, F, 9C, F).—B. Section through the center of a lateral face. Note the characteristically highly channeled endexine.—C. *B. densiflora* (*Abrams 6675*). View on proximal surface in middle of the tetrad. There is considerable similarity with the proximal views of *Boisduvalia subulata* and *Epilobium* (see Skvarla et al., 1976, Pl. 8E, 9B, G). D, E. *Epilobium hirsutum.*—D. View through center of the lateral or polar face. The ektexine appears to consist of slender columellae which support a compact and uniform tectal zone (arrow).—E. Section at proximal face showing extension of viscin threads (arrow) from the ektexine. The upper surface of the endexine immediately beneath the area of viscin threads may represent "outpocketing"; however, it is not clear if this irregularity is actually a portion of the ektexine.—F. *E. cylindricum.* Section beneath aperture protrusion showing two tetrad bridges. Note the granular lower portions of the endexine, characteristic of the aperture region.—G. *E. collinum.* Section on proximal face as well as a cross sectional view of a tightly compound viscin thread. Unless indicated otherwise, the scales equal 1 μm.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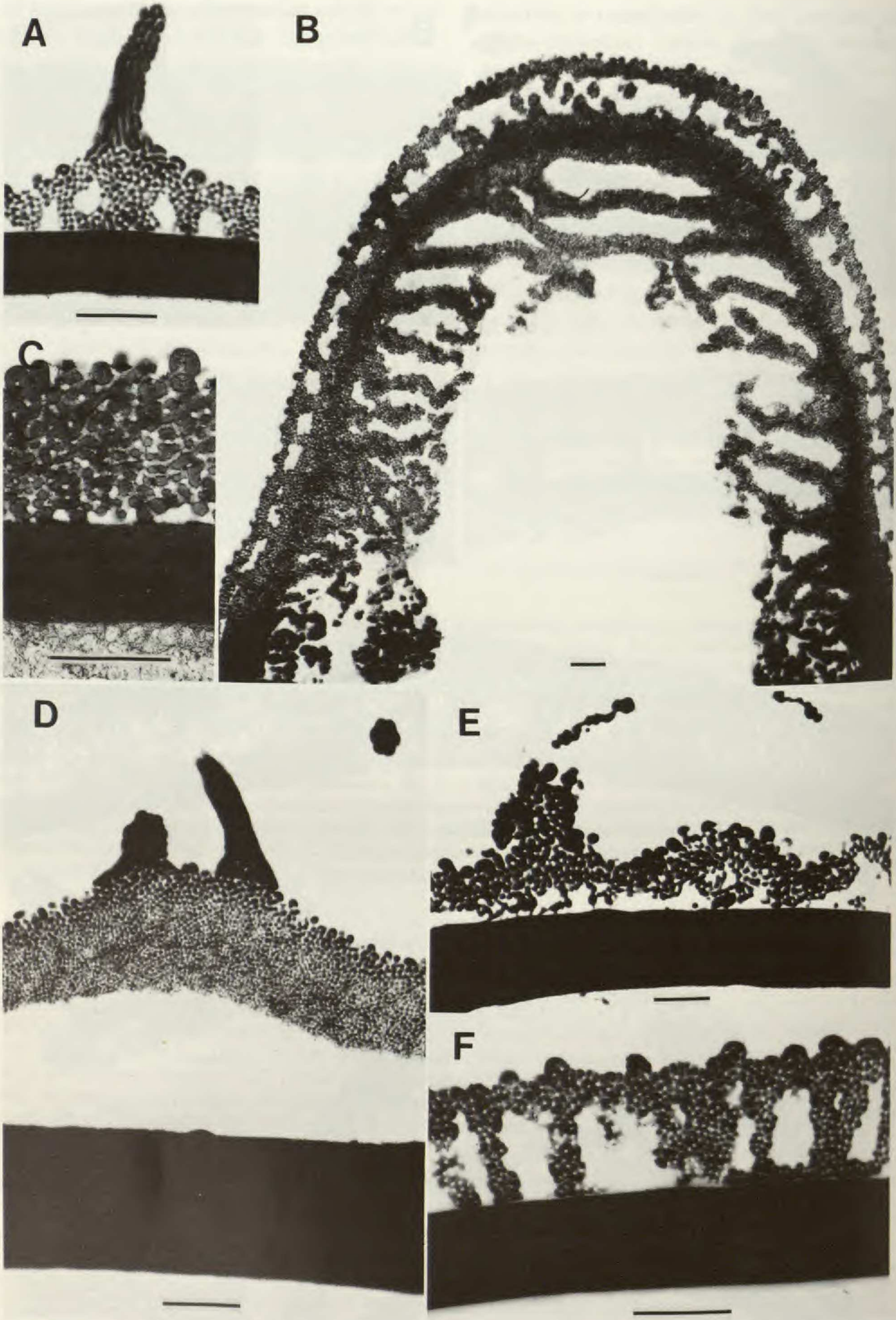
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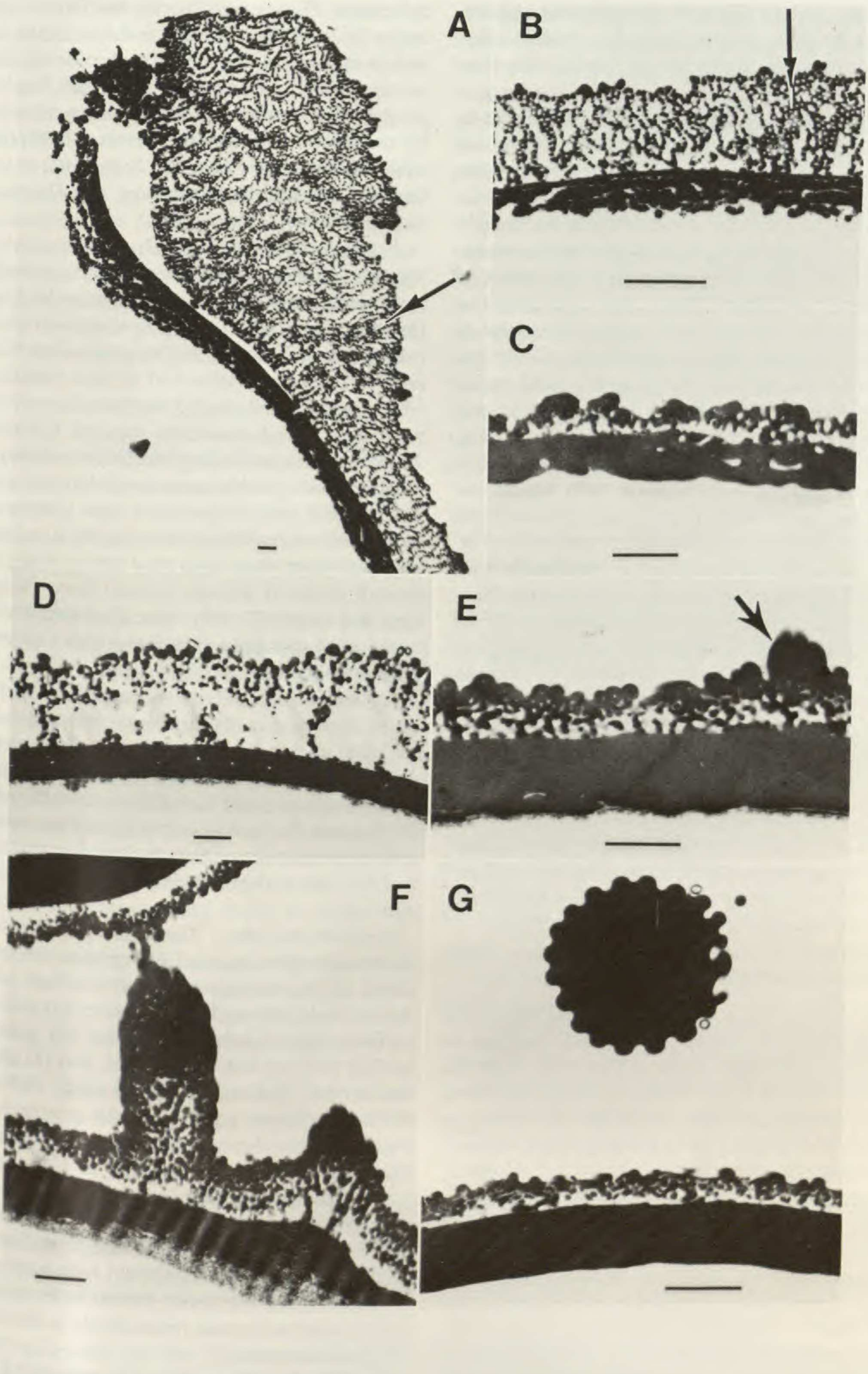
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in certain groups; and an exine surface composed of circular, globular, and elongate or rod-like elements. Prior to this study our feeling was that Onagraceae pollen was unique in the angiosperms, being easily recognizable and difficult to confuse with other groups. After this survey of Myrtales pollen our ideas have not changed: Onagraceae pollen morphology is distinctive in the order. In a remote sense—that is, by considering the extremely thick endexine, surface sculpturing, and protruding apertures—the pollen of *Ludwigia* resembles *Trapa* (see discussion in Trapaceae), although there are no difficulties in recognizing these taxa. A distant similarity between Myrtaceae and Onagraceae pollen exists, particularly in those grains having short colpi (compare *Hauya,* Fig. 50E; *Gongylocarpus,* Fig. 56D; and *Boisduvalia,* Fig. 58A; as well as *Lopezia* of Skvarla et al., 1976, with Myrtaceae SEM on Figs. 41–48). In addition, cross-sections of the subsidiary colpus of *Sonderothamnus* (Fig. 26C, D) of Penaeaceae show a remarkable similarity to those of some taxa of Onagraceae having the spongy ektexine residing directly on the endexine. Lastly, although meridional ridges have been observed on *Ludwigia* pollen (*L. alternifolia,* Fig. 58F), there is no confusing this genus with other taxa in the Myrtales also possessing meridional ridges.

SUMMARY AND CONCLUSIONS

Based on pollen morphology, the families that are considered to be the core members of the Myrtales (Dahlgren & Thorne, 1984) form a relatively cohesive group with the exceptions of Trapaceae, Myrtaceae, and Onagraceae. Each family is summarized below.

1. Lythraceae. The taxa examined from this family show the greatest amount of variation in pollen morphology in the entire order, with diversity evident at all levels: (1) shape (in lateral view: oblate-suboblate, spheroidal-subprolate, or spheroidal; in polar view: triangular-goniotreme, triangular-pleurotreme, triangular to hexagonal, or circular); (2) apertures (tricolpoidorate, tricolporate, tricolporate-syncolpate, or porate); (3) subsidiary colpi (0, 3, or 6); (4) sculpture (striate, striate-spinulate, psilate, or verrucate-rugulate); and (5) structure (normal ektexine-endexine layers, highly reduced or complex columellae). *Punica granatum* (subfam. Punicoideae) is similar to *Lagerstroemia* (Lythroideae) in the triangular shape (polar view) resulting from three meridional ridges. *Punica protopunica* has faint subsidiary colpi, meridional ridges and apertural fields, and thus resembles *Crenea* (Lythroideae). *Sonneratia* (subfam. Sonneratioideae) and *Duabanga* (subfam. Duabangoideae) are characterized by meridional ridges and apertural fields (true subsidiary colpi are absent). *Sonneratia* is similar to *Lafoensia* (Lythroideae), and *Duabanga* to *Diplusodon* (Lythroideae).

2. Trapaceae. This family is unique in having colpi hidden within the protruding, swollen aperture domes of sharply triangular pollen grains (in polar view) and in having three meridional ridges that are united at the poles. The ridges pass over the apertures and in this respect, as well as in structure, they differ from the meridional ridges found elsewhere (e.g., in *Lafoensia, Lagerstroemia,* or *Ludwigia*). *Trapa* remotely resembles *Ludwigia* (Onagraceae) in having a granular-beaded surface sculpture, and Onagraceae in general in exine structure (very thick endexine and indistinct foot layer and columellae), but overall *Trapa* is sharply distinct from Onagraceae and from other Myrtales. One sample of *T. natans* showed linked pollen grains indicating possible polyads.

3. Oliniaceae. The five taxa examined all show two unique features: asymmetrical colpi with unequal arms extending into the opposite polar faces and half subsidiary colpi that are present on only one polar face. *Olinia* resembles some Penaeaceae in having a psilate pollen surface, and in exine structure (a very thick foot layer and tectum, and a thin columellae-infratectal granular layer).

4. Combretaceae. The taxa examined have diverse morphology and five groups are recognized: (1) heterocolpate, (2) heterocolpate with a distinct echinate surface sculpture, (3) echinate surface without subsidiary colpi, (4) punctate surface without subsidiary colpi, and (5) reticulate surface without subsidiary colpi. Pollen in the heterocolpate group indicates general similarities to some Penaeaceae, Crypteroniaceae, and Melastomataceae.

5. Alzateaceae. Alzatea verticillata is similar in pollen characteristics to *Axinandra* and *Dactylocladus* (Crypteroniaceae) and *Rhynchocalyx* (Rhynchocalycaceae). Indistinct subsidiary colpi or intercolpar concavities appear to be present. In fine structure some resemblance is shown to Chrysobalanaceae.

6. Rhynchocalycaceae. The pollen of *Rhynchocalyx lawsonioïdes* is tricolporate and heterocolpate with three subsidiary colpi. In these and other characteristics the pollen of *Rhynchocalyx* is similar to that of Alzateaceae, *Dactylocladus* and *Axinandra* (Crypteroniaceae), *Dissocheata* (Melastomataceae) and *Lumnitzera* (Combretaceae).

7. Penaeaceae. The taxa examined are heterocolpate with tri- and tetracolporate pollen; *Glischrocolla* has 5-colporate pollen. Exomorphic resemblances are with Melastomataceae (*Tristemma, Dissotis*), Combretaceae (*Combretum, Quisqualis*), and Crypteroniaceae (*Dactylocladus*). Endomorphic resemblance is striking with Oliniaceae and *Dactylocladus* of Crypteroniaceae.

8. Crypteroniaceae. Dactylocladus and *Axinandra* are heterocolpate and can be favorably compared with some Lythraceae, Melastomataceae, Combretaceae, Penaeaceae, and perhaps in a general way with much of the Myrtales. *Crypteronia* differs from most Myrtales in having dicolporate pollen with two intercolpar concavities.

9. Melastomataceae. Pollen of the taxa can be divided into three basic types: (1) heterocolpate with subsidiary colpi alternating with colpi, (2) "heterocolpate" with intercolpar concavities alternating with colpi, and (3) tricolporate. The first group resembles several of the heterocolpate Combretaceae. Also in this first group are several genera often segregated as Memecylaceae, but they are not delimited as a group within the heterocolpate Melastomataceae. *Tococa spadiciflora* occurs as polyads, the only member of the family to the present time found to occur this way, and along with some *Ludwigia* of Onagraceae (and perhaps *Trapa natans* as discussed above), the only taxa with polyads in the Myrtales. Similarly, *Miconia melanotricha* is the only species in the family reported to have pollen in tetrads.

10. Myrtaceae. An essentially consistent morphology is found in all taxa examined. The markedly triangular (in polar view) pollen is divided, based in part on previous reports, into three groups defined by colpus morphology: (1) longicolpate (no intercolpar concavities), (2) syn- and parasyncolpate with and without intercolpar concavities, and (3) brevi- or brevissimicolpate (no intercolpar concavities). Pollen of *Myrtus communis* and *Psidium littorale* is found frequently as tetrads, the only other record in Myrtales other than Onagraceae (some species of *Ludwigia, Epilobium, Boisduvalia, Zauschneria,* and *Camissonia*) and *Miconia melanotricha* of Melastomataceae. *Psiloxylon* has large apocolpia but overall is similar to most Myrtaceae pollen in group (2). *Heteropyxis* likewise is not distinguished within the second group. Pollen of Myrtaceae is not clearly comparable with any other pollen in the Myrtales.

11. Onagraceae. The pollen of the taxa examined is variable within the family but, like Myrtaceae, is without any close similarity in the Myrtales. The distinctive characters are circular to triangular central body with markedly to slightly protruding apertures; globular (granular), rod-like (elongate), or rugulate surface elements; tetrads and polyads in addition to monads; viscin threads, and thick endexine and essentially spongy-paracrystalline ektexine usually lacking columellae and always lacking a foot layer.

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